Quasi-patterns produced by a Mexican Hat coupling of quasi-cycles

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Abstract. A family of stochastic processes has quasi-cycle oscillations if its otherwise-damped oscillations are sustained by noise. Such a family forms the reaction part of a stochastic reaction-diffusion system when we insert a local Mexican Hat-type, difference of Gaussians, coupling on a one-dimensional and on a two-dimensional lattice. We find spatial patterns of oscillating quasi-cycles that resemble Turing patterns, called quasi-patterns. Specific properties of these patterns, such as local phase synchronization, can be predicted from the parameters of the reaction and of the Mexican Hat coupling. When the damping parameters of the reaction and diffusion parts are small and balanced, phase synchronization vanishes but amplitude patterns persist. These results extend our knowledge of the behaviour of coupled neural field equations and its dependence on stochastic fluctuations.

Keywords: difference-of-Gaussians, Mexican Hat, quasi-cycles, quasi-patterns, neural oscillators, stochastic neural field, excitation-inhibition interaction, Kuramoto model.

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1. Introduction

The celebrated book of Y. Kuramoto (Kuramoto, 1984) begins with a description of a reaction-diffusion system “...obtained by adding some diffusion terms to a set of (first order) ordinary differential equations.” He notes that “...the propagation of the action potential in nerves and nerve-like tissues is known to obey this type of equation.” Continuing, he states that the important feature of reaction-diffusion fields, not shared by fluid dynamical systems, is that the total system can be viewed as an assembly of a large number of local systems that are all ‘diffusion coupled’ to each other. He assumed that if one of these local systems were isolated, it would display a persistent limit cycle. “Thus the total system may be imagined as forming a diffusion-coupled field of similar limit cycle systems.” ((Kuramoto, 1984), page 1). A primary result was that coupling of limit cycle phases over the entire field produces synchronization of those phases over the entire field, if coupling is sufficiently strong.
Our topic in this paper is an extension of this viewpoint of Kuramoto and some of his results to what we will term a stochastic reaction-coupling system, to recognize that the diffusion is accomplished by a local coupling of the reaction components of the stochastic system. In our stochastic extension, Kuramoto’s limit cycles of individual components are replaced by otherwise damped temporal oscillations that are sustained by noise. Such stochastic oscillations are called quasi-cycle oscillations (Bressloff, 2010; P. Greenwood, McDonnell, & Ward, 2015). Kuramoto’s Laplacian coupling operator is replaced by a Mexican-Hat-coupling operator. The resulting spatial waves interact with reaction-plus-noise-generated temporal waves to form spatial patterns of synchronization.

Kuramoto concentrated on fields of phase oscillators with the amplitude of oscillation removed from consideration. We explore, in addition, the effects of the coupling on the associated amplitude processes.

Our local coupling is implemented by a difference-of-Gaussians, or Mexican Hat, operator, inspired by a neural field where each neuron is excited by close neighbours and inhibited by somewhat less close neighbours. We use Itô’s Lemma to derive stochastic partial differential equations for the coupled phase and coupled amplitude components of our neural field.

In certain parameter regions reaction-diffusion equations generate Turing patterns. It is known (Butler & Goldenfeld, 2011; McKane, Biancalani, & Rogers, 2014) that stochastic reaction-diffusions can generate quasi-patterns in space-time in parameter regions where the uniform solution of the corresponding reaction-diffusion has unstable modes that are damped in the deterministic version of the system, and that therefore fails to produce Turing patterns. Motivated by the existence of such examples, in (P. E. Greenwood & Ward, 2017) we explored how certain sample path properties of simple stochastic neural fields depend on coupling strength and Mexican Hat parameters. Here we extend the study to evolving random fields where reaction terms produce quasi-cycles that are then coupled. An essential difference from several of our references is that we couple, not deterministic cycles, but quasi-cycles, damped oscillations sustained by noise. The patterns produced by local coupling of quasi-cycles are called quasi-patterns. They are also sustained by noise. We produce and analyse simulations of such patterns from our reaction-coupling system.

The primary mathematical results of this paper are: (a) We use Itô’s Lemma to derive stochastic differential equations for the temporal amplitude and phase processes corresponding to stochastic reaction-coupling processes. (b) We extend the BG (Baxendale & Greenwood, 2011) factorization of quasi-cycle processes, when the reaction and diffusion terms in the system are balanced, to the case of weakly coupled fields.

It turns out, in this case, that the standard Ornstein-Uhlenbeck process in the factorization of (Baxendale & Greenwood, 2011) is replaced in our stochastic reaction-coupling process by a stochastic neural field, a standard Ornstein-Uhlenbeck field with Mexican Hat coupling. Itô’s Lemma then translates the Euclidean system into stochastic differential equations for the space-time amplitude and phase processes.
The factorization results in the quasi-cycles themselves not being coupled. Rather, the BG factorization gives rise to coupling only in the neural field expression, not involving the deterministic rotation in time that represents the quasi-cycles. This balanced, slowly damping and weakly-coupled system gives us an alternative model possibility. We call it simply the ‘balanced case’.

Simulation of the amplitude and phase processes in the two cases reveals previously unseen ‘sample path’ properties. In the unbalanced case (a) spatial quasi-patterns of synchronization appear among phases of the temporal oscillations, with degree of synchronization increasing with coupling strength, and (b) corresponding spatial quasi-patterns appear also in the amplitudes of the temporal oscillations. In the balanced and factored model, a similar but quantitatively different quasi-pattern appears in the amplitudes but no pattern appears in the phases. This difference might prove to be important when modeling stochastic neural fields in brains.

In Section 2 we describe our basic model and use Itô’s Lemma to derive the stochastic differential equations for phase and amplitude components of the solution. Section 3 is devoted to the same reaction-coupling system but with a specific balance between the reaction and diffusion terms. In Section 4 we describe the results of simulations of the SDEs in one and two spatial dimensions, and in Section 5 we discuss these results and our models in the context of other models that involve Mexican Hat coupling and neural field equations.

2. A one- or two-dimensional (state space) stochastic reaction-coupling system

2.1. The model. Our model is a variety of neural field equation consisting of a family of density dependent Markov processes indexed by \( j = 1, 2, \ldots, N \). We think of \( j \) as indexing points in a spatial lattice in \( \mathbb{R}^1 \) or \( \mathbb{R}^2 \). For each \( j \) we have a linear stochastic process

\[
 dt V_j(t) = -A_0 V_j(t) dt + MG V_j(t) dt + E_0 dW_j(t),
\]

with values in \( \mathbb{R}^2 \), \( V_j(t) = (v_{1j}(t), v_{2j}(t)) \). The matrix \( -A_0 \) has complex eigenvalues \( -\lambda \pm i\omega \) with \( 0 < \lambda \). The processes \( W_j \) are independent \( \mathbb{R}^2 \) Brownian motions. \( M \) is the operator defined by

\[
 M \xi_j(t) = \sum m(i - j)\xi_j(t),
\]

where \( m(j) \) is a discretization of \( m(x) \), a smooth (spherically) symmetric, bounded function with support on a bounded interval, such as the Mexican Hat function \((4.2)\). The operator \( M \) commutes with multiplication by constant matrices. \( M \) represents a local spatial operator: here the difference-of-Gaussians (Mexican Hat) operator or its discrete approximation. In Kuramoto’s field of coupled limit cycle phases \( m(x) \) was constant.

The biological role of \( G \) has been related to the fact that neurons can only fire below their maximum rate, which is theoretically around 500 Hz but practically below about 200 Hz. Our choice of \( G \), convenient for our computations, is:

\[
 G(v_j(t - \Delta t, x)) = \begin{cases} 
 v_j(t - \Delta t, x) & \text{if } |v_j(t - \Delta t, x)| \leq v_{\text{max}}, \\
 0.9v_j(t - \Delta t, x) & \text{if } |v_j(t - \Delta t, x)| > v_{\text{max}}.
\end{cases}
\]
Simulations show that the processes $V_j(t)$ generally increase in $t$. By choosing $v_{\text{max}} = 5$ we have a wide parameter range within which to carry out our numerical studies before the process attains $v_{\text{max}}$ and $G$ comes into play. Hence, we can carry out our stochastic analysis by approximating $G$ by the identity. Such a functional satisfies the Lipschitz and boundedness conditions under which Faugeras and Inglis (Faugeras & Inglis, 2015) assure us of the existence and uniqueness of a non-constant solution to the stochastic neural field equation, on compact time intervals, where $A_0 = I$ in (2.1).

The noise, denoted $dW_j(t)$ is standard temporal Gaussian noise with independent components and is independent for each $j$. With the coefficient $E_0$ the noise term has temporal covariance matrix $\mathbb{E}_0 = E_0 E_0^\top$. Space is wrapped to avoid boundary conditions.

The system (2.1) represents a stochastic perturbation of the linearization around a stable fixed point of a corresponding deterministic system. We could have begun with only the reaction term, $-A_0 V_j(t)dt$, on the righthand side, the reaction equation representing a linearized system of discrete state-space models, such as the predator-prey example in (Baxendale & Greenwood, 2011) or a simple (SIR) epidemic model, or an excitatory-inhibitory neuron population model as will appear later in this paper. Without the coupling term the system (2.1) produces a collection of stochastically identical quasi-cycles with basic frequency $\omega$.

In (P. E. Greenwood & Ward, 2017) we studied the conditions under which we can expect to see spatial quasi-patterns in the values produced by stochastic neural field equations that have only simple damping as a reaction term in the reaction-coupling system. In particular, there were no quasi-cycle oscillators. In what follows we derive expressions for the evolution of a stochastic reaction-coupling system in which the reaction parts, with stochasticity, do produce quasi-cycle oscillations. Quasi-patterns appear in both amplitude and phase components of these oscillations. We extend the Kuramoto (Kuramoto, 1984) approach to such systems in three ways: (a) our model has quasi-cycle oscillators instead of limit cycle oscillators, (b) we consider both phase and amplitude, and (c) we couple the oscillators using a local Mexican Hat (difference-of-Gaussians) coupling instead of a Laplacian. Itô's Lemma produces local couplings of phases and amplitudes in our stochastic system, analogous in form to the couplings described in (Daffertshofer & van Wijk, 2011) for deterministic systems.

2.2. Stochastic phase and amplitude equations. Our computations of the phase and amplitude equations corresponding to the neural field equation (2.1), with $G = I$, are simplified by beginning with the matrix $A_0$ changed to normal form. Let $Q$ be a 2x2 matrix such that

$$Q^{-1}(-A_0)Q = \begin{pmatrix} -\lambda & \omega \\ -\omega & -\lambda \end{pmatrix} := \Lambda.$$  

Such a matrix is

$$Q = \begin{pmatrix} -\omega & \lambda - A_{011} \\ 0 & -A_{021} \end{pmatrix}.$$ 

We change variables in (2.1), with $G$ replaced by $I$ as noted, putting

$$Y_j(t) = Q^{-1}V_j(t),$$
to obtain
\begin{equation}
\dot{Y}_j(t) = AY_j(t)dt + MY_j(t)dt + EdW_j(t),
\end{equation}
where $E := Q^{-1}E_0$. For simplicity in our computations we take the covariance matrix $E = I$. Later we comment on the effect of this choice. We will regard (2.7) as our model, with $Y_j(t) = \begin{pmatrix} u_j(t) \\ v_j(t) \end{pmatrix}$. Using Itô’s Lemma we obtain the following stochastic equations for $\theta_j = \arctan(v_j/u_j)$ and $Z_j = (u_j^2 + v_j^2)^{1/2}$ (see Appendices A and B):

\begin{align}
\dot{\theta}_j &= \omega dt \\
&+ \left[ \sum_{l=1}^{N} \frac{Z_l(t)C_{jl} \sin(\theta_j(t) - \theta_l(t))}{Z_j(t)} \right] dt \\
&+ \frac{db(t)}{Z_j(t)},
\end{align}

\begin{align}
\dot{Z}_j &= \left( \frac{1}{2Z_j(t)} - \lambda Z_j(t) \right) dt \\
&+ \left[ \sum_{l=1}^{N} C_{jl}Z_j \cos(\theta_j(t) - \theta_l(t)) \right] dt \\
&+ dW_j(t),
\end{align}

where $b(t)$ is Brownian motion on the unit circle, and $C_{jl}$ represents the Mexican Hat coupling, $M$, defined over a specific range of the spatial lattice.

### 3. An approximate factorization of the stochastic reaction-coupling neural field equation

In this section we explore a version of our stochastic neural field model (2.1) that leads to phase and amplitude equations similar to (2.8) and (2.9), but that exhibit different patterns in the phase and amplitude fields. We are inspired by the following result about quasi-cycles that appeared in (Baxendale & Greenwood, 2011).

Consider the processes $\tilde{Y}_j(t)$ that satisfy the SDE (2.1) with no coupling, that is with $M = 0$:

\begin{equation}
\dot{Y}_j(t) = A\tilde{Y}_j(t)dt + dW_j(t),
\end{equation}

where $A$ is given by (2.4). For each $j$, without coupling, we have, following from Theorem 1 of (Baxendale & Greenwood, 2011) for small values of $\lambda/\omega$,

\begin{equation}
\tilde{Y}_j(t) \approx \tilde{\tilde{Y}}_j(t) := \frac{\sigma}{\sqrt{\lambda}} R_{-\omega t} S_j(\lambda t).
\end{equation}

Here $R_{-\omega t}$ is a rotation matrix

\begin{equation}
R_s = \begin{pmatrix}
\cos(s) & -\sin(s) \\
\sin(s) & \cos(s)
\end{pmatrix}
\end{equation}
and $S_{lj}(t)$ is a pair of independent standard Ornstein-Uhlenbeck processes, $S_{lj}(t) = (S_{1lj}(t), S_{2lj}(t))^\top$, 

\begin{equation}
\label{eq:3.4}
dS_l = -S_{lj}dt + dW_{lj}, \quad l = 1, 2.
\end{equation}

Notice that in the process $\tilde{Y}_j(t)$, the deterministic rotation at rate $-\omega t$ factors from the stochastic part of the process. The process $\tilde{S}_j(t)$ has stochastic phase process $\phi_j = \arctan(S_{2lj}/S_{1lj})$ and stochastic amplitude process $Z_j = \sigma \sqrt{\lambda (S_{1lj}^2 + S_{2lj}^2)^{1/2}}$. We can write the approximation (3.2) in terms of stochastic amplitude and phase processes.

The matrix $A$ is the same for all processes (3.2) parametrized by $j$, so that we have the same eigenvalues $-\lambda \pm i\omega$ for them all. One can use Itô’s Lemma (see Gardiner (Gardiner, 1990)) to render the pair of independent standard Ornstein-Uhlenbeck processes, and hence the factorization (3.2), in polar coordinates, obtaining, for each $j = 1, 2, \ldots N$ (without coupling among subpopulations), for the phase of the approximating process, $\tilde{V}_j(t)$,

\begin{equation}
\label{eq:3.5}
\theta_j(t) = -\omega t + \phi_j(\lambda t)
\end{equation}

with $\phi_j$ defined by

\begin{equation}
\label{eq:3.6}
d\phi_j(t) = \frac{db_j(t)}{Z_j(t)},
\end{equation}

and for the amplitude,

\begin{equation}
\label{eq:3.7}
Z_j(t) = \sigma \sqrt{\lambda} \tilde{Z}_j(t)
\end{equation}

where

\begin{equation}
\label{eq:3.8}
d\tilde{Z}_j(t) = \left( \frac{1}{2Z_j(t)} - \tilde{Z}_j(t) \right) dt + dW_j(t).
\end{equation}

The processes $b_j, W_j$ are independent Brownian motions, the $b_j$ on the unit circle.

By following the proof of approximation (3.2) in (Baxendale & Greenwood, 2011) we can obtain a corresponding approximation to the solution of the reaction-coupling equation (2.7) for small $\lambda/\omega$. In order to obtain a non-degenerate result, we assume that the coupling term is of the same order as the reaction term in (2.7). To express this hypothesis, we write our model as

\begin{equation}
\label{eq:3.9}
dt Y_j(t) = AY_j(t)dt + \frac{\lambda}{\omega} MY_j(t)dt + dW_j(t).
\end{equation}

We call this the balanced case. The following argument parallels the proof of Theorem 1 in (Baxendale & Greenwood, 2011), a limit theorem as $\lambda/\omega$ goes to zero.

Because $\mathbb{E} = \mathbb{I}$, $\sigma = 1$, where $\sigma$ is defined by

\begin{equation}
\label{eq:3.10}
\sigma^2 := \frac{1}{2} tr(\mathbb{B}) = \frac{1}{2} (\mathbb{B}_{11} + \mathbb{B}_{22}) = \frac{1}{2} \sum_{i,j=1}^{2} E_{ij}^2.
\end{equation}

We wish to transform (3.9) so that the matrix $A = (-\lambda \quad \omega \quad -\lambda)$ in the drift term becomes the identity. As a first step we write

\begin{equation}
\label{eq:3.11}
Y_j(t) = \mathbb{E} - \omega t \tilde{Z}_j(t).
\end{equation}
From the stochastic partial differential equation (3.9) we obtain using Itô’s Lemma

\[ d_t Z_j(t) = \]

\[ -\lambda Z_j(t) dt + \frac{\lambda \omega}{\omega} \mathbb{R}_{\omega t} \mathbb{R}_{-\omega t} Z_j(t) + \mathbb{R}_{\omega t} d\mathcal{W}_j(t). \]

(3.12)

Finally, we rescale time and the value space of \( Z \) according to

\[ U_j(t) = \frac{\sqrt{\lambda}}{\sigma} Z_j(t/\lambda), \]

(3.13)

where \( \sigma \) is defined in equation (3.10). We use the integrated form of \( U_j(t) \), the change of variables \( s = u/\lambda \), and the fact that \( \mathbb{R}_{\omega t} \) is constant in \( j \), to compute

\[ U_j(t) - U_j(0) = \frac{\sqrt{\lambda}}{\sigma} \left[ -\lambda \int_0^{t/\lambda} Z_j(s) ds + \lambda \int_0^{t/\lambda} \mathbb{R}_{\omega s} \mathbb{R}_{-\omega s} M Z_j(s) ds + \int_0^{t/\lambda} \mathbb{R}_{\omega s} d\mathcal{W}_j(s) \right]. \]

(3.14)

where \( \mathcal{W}(s) = \sqrt{X\mathcal{W}(s/\lambda)} \) is ‘another’ standard Brownian motion. Inserting the definition of \( s \) we obtain

\[ U_j(t) - U_j(0) = \frac{\sqrt{\lambda}}{\sigma} \left[ -\int_0^t Z_j(u/\lambda) du + \int_0^t M Z_j(u/\lambda) du + \frac{1}{\sqrt{\lambda}} \int_0^t \mathbb{R}_{\omega u/\lambda} d\mathcal{W}_j(u) \right] \]

\[ = -\int_0^t U_j(u) du + \int_0^t M U_j(u) du + \frac{1}{\sigma} \int_0^t \mathbb{R}_{\omega u/\lambda} d\mathcal{W}_j(u). \]

(3.15)

So \( U_j(t) \) is a process satisfying (we add the notation \( \mathbb{U}^\lambda \) for clarity)

\[ d_t \mathbb{U}^\lambda_j(t) = -\mathbb{U}^\lambda_j(t) dt + M \mathbb{U}^\lambda_j(t) dt + \frac{1}{\sigma} \mathbb{R}_{\omega t/\lambda} d\mathcal{W}_j(t). \]

(3.16)

Following essentially the same proof as in Theorem 1 of (Baxendale & Greenwood, 2011) we can see that as \( \lambda/\omega \to 0 \), the process \( \mathbb{U}^\lambda(t, x) \) converges weakly on time intervals \([0, T]\) and compact sets of \( x \) to a solution of

\[ d_t U_j(t) = -U_j(t) dt + MU_j(t) dt + d\mathcal{W}_j(t). \]

(3.17)

As in (Baxendale & Greenwood, 2011), reversing the sequence of changes of variables and taking \( \lambda \) small we have the approximation

\[ \mathbb{V}_j(t) \approx \tilde{\mathcal{V}}_j(t) = \frac{\sigma}{\sqrt{\lambda}} \mathbb{R}_{-\omega t} U_j(\lambda t), \]

(3.18)

where \( U_j(t) \) is a solution of equation (3.17).

In Appendix C we derive the stochastic equations for the phase and amplitude processes of (3.18):

\[ \theta_j(t) = -\omega t + \phi_j(\lambda t), \]

\[ \phi_j(t) = \int_0^t \theta_j(s) ds, \]

(3.19)
where \( \phi_j(t) \) satisfies

\[
d\phi_j(t) = \left[ \sum_{l=1}^N Z_l(t) C_{jl} \sin(\phi_j(t) - \phi_l(t)) \right] dt + \frac{db(t)}{Z_j(t)},
\]

(3.19)

\[
Z_j(t) = \frac{\sigma}{\sqrt{\lambda}} \bar{Z}_j(\lambda t),
\]

where \( d\bar{Z}_j(t) \) satisfies

\[
d\bar{Z}_j = \left[ \frac{1}{2\bar{Z}_j(t)} - \bar{Z}_j(t) \right] dt + \left[ \sum_{l=1}^N C_{jl} \bar{Z}_j(t) \cos(\phi_j(t) - \phi_l(t)) \right] dt + dW_j(t).
\]

(3.20)

The approximation (3.18) of the solution of the reaction-coupling equation (3.9) tells us that the rotation in time, associated with the complex eigenvalues of \( A \), factors apart from the stochastic part of the process, \( U(\lambda t) \), where \( U \) generated by (3.17). The process \( U(t) \) is of the form called a stochastic neural field (Faugeras & Inglis, 2015)(P. E. Greenwood & Ward, 2017). We have shown in (3.18) that (3.9) produces a product of an evolving spatial pattern process and a deterministic rotation in time that arises from the quasi-cycles. This means that the quasi-cycles in (3.18) are not diffusion coupled in the Kuramoto sense as happens in (2.8) and (2.9). Thus, the spatial patterns generated by (3.19) and (3.20) will be different from those generated by (2.8) and (2.9). In particular, because the phases of the quasi-cycles, \( \theta(t) \), are not coupled by the Mexican Hat operator in (3.19), they will not be synchronized. Hence, spatial patterns should not appear in plots of phases obtained from simulating (3.19), but spatial patterns of amplitudes from (3.20) should appear.

There follows our numerical study of the properties of the discrete Mexican-Hat-coupled system of quasi-cycle oscillators. We vary the Mexican Hat operator in several ways, in both one and two spatial dimensions. We are interested in the question: how do spatial waves produced by local coupling combine with point-based temporal quasi-cycles over an evolving random field of quasi-patterns? We display plots of sample paths of the systems \( \mathcal{V}(t,x) \) defined by (2.1) and (3.9) via the discretized polar systems (2.8), (2.9), plots of (3.19), (3.20), with specific parameters, in one spatial dimension, and fixed-time plots in two dimensions for (2.8) and (2.9).

4. Numerical Results

In order to study the consequences of the discrete Mexican Hat coupling of noise-driven oscillators (quasi-cycles), we solved numerically the relevant SDEs, with parameters given in the next section, using the Euler-Maruyama discretization method (Kloeden & Platen, 1992). We varied the noise strength and the coupling strength between the systems to generate the spatial patterns displayed. In one spatial dimension we simulated the local coupling of 128 quasi-cycle processes with periodic boundary. In two dimensions we simulated a 100x100 (=10,000 processes) lattice with a neutral (no coupling) boundary. The basic procedure was the same for all computations. A discretized difference-of-Gaussians operator (Murray, 1989) was multiplied by the coupling strength, \( c \geq 1 \), to create a Mexican Hat operator (see (P. E. Greenwood & Ward, 2017)). This operator was then applied to the
value of the phase and the amplitude of the processes at the previous time point successively across space to compute the contribution of the coupling with neighboring processes to the next increment. The current value of each phase and each amplitude was computed by adding the coupling contribution to the temporal progression of each process at each time point. This was continued for the indicated number of time points. The time step was made small, 0.00005 sec, in order to avoid problems with stiff solutions. Noise was always i.i.d., mean zero Gaussian noise with standard deviation as described. \( Y_{\text{max}} \) in \( \mathbb{G} \) was set to 5.

4.1. Stochastic reaction-coupling field in one spatial dimension: system (2.8), (2.9). Here for the reaction term we have in mind a family of models often considered in mathematical neuroscience where populations of excitatory (E) and inhibitory (I) neurons interact according to a scheme that is an example of our basic model (2.1). Suppose we have a family of \( N \) excitatory-inhibitory subpopulation models indexed by \( j = 1, 2, \ldots, N \), as in (P. Greenwood, McDonnell, & Ward, 2016; Kang, Shelley, Henrie, & Shapley, 2010). For each \( j \) the model (2.1) will be a copy of equation (1) of (P. Greenwood et al., 2016):

\[
\tau_E dV_E(t) = (-V_E(t) + S_{EE} V_E(t) - S_{EI} V_I(t)) dt + \sigma_E dW_E(t) \\
\tau_I dV_I(t) = (-V_I(t) - S_{II} V_I(t) + S_{IE} V_E(t)) dt + \sigma_I dW_I(t).
\]

In (4.1) \( W_E, W_I \) are independent, standard Brownian motions. \( S_{EE}, S_{II}, S_{IE}, S_{EI} \geq 0 \) are constants representing the efficacies of excitatory or inhibitory synaptic connections to post-synaptic neurons within each separate population, as indicated by the notation, with \( S_{IE} \) representing input to inhibitory from excitatory neurons. These parameters, along with the time constants, \( \tau_E, \tau_I \), and amplitudes of the Brownian motions, \( \sigma_E, \sigma_I \), determine the oscillatory behaviour of the system and in particular its resonant frequency of oscillation. When (4.1) is expressed in the notation of (2.1), as in (P. Greenwood et al., 2015),

\[
-A_0 = \begin{pmatrix} (1-S_{EE})/\tau_E & S_{EI}/\tau_E \\ -S_{IE}/\tau_I & (1+S_{II})/\tau_I \end{pmatrix}.
\]

The resonant frequency of oscillation, \( \omega \), arises from the complex eigenvalues, \(-\lambda \pm \omega\), of \( A_0 \) (see (P. Greenwood et al., 2015) for a complete discussion of this model). We chose a parameter set (see Table 1) where the oscillation is narrowband and thus has a distinct phase even though it arises from a stochastic process (P. Greenwood et al., 2015).

An essential point is that without the noise, i.e., with \( \sigma_E = \sigma_I = 0 \), the temporal oscillations damp to zero. With small noise the oscillations are sustained and are called quasi-cycles. Also, in (2.8) or (3.19), if \( Z \) were allowed to become very large, \( db/Z \) would be very small, and the rotation, \( \omega dt \), would dominate and a limit cycle would form. Thus we only have quasi-cycles when \( Z \) is fairly small, \( Z < Z_{\text{max}} = \nu_{\text{max}} \), so that \( db/Z \) doesn’t approach zero. In all simulations we monitored \( Z \) to ensure that the inequality held.

Note that (4.1) can be interpreted as applying to a single pair of neurons, or to a single oscillatory system characterized by a particular resonant frequency. Copies of processes (4.1), indexed by \( j \) denoting location on a discrete lattice in \( \mathbb{R}^1 \) or \( \mathbb{R}^2 \), coupled by the Mexican Hat operator as in (2.7) and (3.9) and expressed in polar coordinates in (2.8), (2.9) and (3.19), (3.20), comprise our reaction-coupling dynamics. In (2.8), (2.9), the reaction and noise terms produce quasi-cycles that are then coupled by the Mexican Hat operator. In (3.19), (3.20), however, the
quasi-cycles are not coupled; only the Ornstein-Uhlenbeck processes appearing in (3.2), \( S_j(\lambda t) \) are coupled.

We considered 128 such processes, arranged in a ring (periodic boundary condition), all oscillating at the resonant frequency \( \omega = 437.72 \) \( \text{rad/s} \), similar to the system we studied for the Kuramoto model (P. Greenwood et al., 2016). For convenience, we began each realization with the phases of the 128 systems distributed uniformly between 0 and \( \pi \), and the amplitudes distributed as 0.5 plus 0.1 times a sample from the uniform \((0,1)\) distribution. This ensured that any synchronization of phases, or spatial patterns of amplitudes, would be produced by the Mexican Hat operator and not because the processes were started in that state.

We employed as the coupling operator (Murray, 1989) a (truncated), discretized, difference of Gaussian functions (Mexican Hat), written in continuous space variable, \( x \), as

\[
m(x) = b_1 \exp \left[ -\left( \frac{x}{d_1} \right)^2 \right] - b_2 \exp \left[ -\left( \frac{x}{d_2} \right)^2 \right], \quad b_1 > b_2, d_2 > d_1.
\]

In (4.2) \( b_1, b_2 \) are the heights of the Gaussian functions at \( x = 0 \), and \( d_1, d_2 \) are their dispersions. We used parameters \( b_2 = d_1 = 1.0 \) and \( b_1, d_2 \) with various values as indicated in our figures. The values of the latter two parameters determine the wave number of the spatial pattern produced in our system. In the discrete version used in computation, the Mexican Hat (4.2) is represented by numbers \( C_{jl} \). Outside the region of the Mexican Hat \((j - l > 31)\), the \( C_{jl} \) of (2.8) and (2.9) were set to zero. In our computations the values of \( C_{jl} \) were sometimes multiplied by a number \( c \geq 1 \), to magnify what we call the ‘coupling strength’. This is necessary when the maximum of the PSD of the MH operator is lower than the value required to create excitable states and hence a visible pattern (see (P. E. Greenwood & Ward, 2017; Murray, 1989)). It can also affect the speed of pattern development, as will be shown later in this section.

In order to illustrate spatial patterns, for each set of parameter values we display a representative realization of the evolving random field consisting of the paths of all 128 processes, both amplitude and phase, positioned evenly over the ring, with the ring flattened out. We also display, for those realizations, the spatial power spectral density (PSD) as a stochastic process in \( t \), and a second measure we term \( F \). \( F \) is a function of \( t \) and \( x \), written as

\[
F(t,x) = \frac{1}{500 \ j_{max}} \sum_{s \in \text{timeblock}} \sum_{y=1}^{j_{max}} |Y(s, y + x) - Y(s, y)|
\]

where \( x \), or \( j \) in our discrete space variable, is called a spatial offset and \( j_{max} \) is the distance across the array for which we are computing \( F \). In our computations \( j_{max} \) was fixed at \( j_{max} = 64 \) because the period of the spatial pattern never exceeded this value. In the computation \( x \) is increased progressively across the spatial array. Thus, in time blocks where the average difference \( |Y(t, y + x) - Y(t, y)| \) is large, the value of \( F \) is correspondingly increased. Local maxima in the plot of \( F(t,x) \) occur wherever the spatial offset \( x \) matches half the period of the spatial pattern. For both the spatial PSD and the computation of \( F \) we coarse-grained time, considering 500-iteration time blocks: 1-500, 750-1250, 1750-2250, ..., 9501-10000. For the spatial PSD we averaged the amplitude of each process over the 500-iteration block and then computed the PSD on the resulting spatial array. In computing \( F(t,x) \) we
averaged over $T = 500$ iterations as in (4.3). Thus a plot of $F$, a realization of a stochastic process in $t$ and $x$, tells us about the periodicity of the spatial patterns around position $x$ near time $t$.

Table 1. Parameters used in simulations and for figures.

| Variable | Value | Units          |
|----------|-------|----------------|
| $S_{II}$ | 0.1   | dimensionless |
| $S_{EE}$ | 1.5   | dimensionless |
| $S_{EI}$ | 1.0   | dimensionless |
| $S_{IE}$ | 4.0   | dimensionless |
| $\tau_E$ | 3     | ms            |
| $\tau_I$ | 6     | ms            |
| $\lambda$ | 8.333 | 1/seconds     |
| $\omega$ | 437.72 or 69.66 | radians per second or Hz |
| $\lambda/\omega$ | 0.019 | dimensionless |
| $\sigma$ | 6.85  | mV            |
| $\Delta t$ | 0.00005 | seconds       |

Figure 1 displays the results of an illustrative simulation of the 1D model that clearly shows the existence of spatial quasi-patterns in both amplitude and phase. On each position $x$, or $j$ in our discrete notation, in the ring sits a process that generates a (temporal) quasi-cycle at approximately 70 Hz. So the amplitudes and phases displayed at the various positions, $x$, over time in Figure 1 are those of the (temporal) quasi-cycle at that position. For example, the amplitudes of the components near $x = 80$ are large compared to those at nearby points beginning at about iteration 6000 and continuing until the end of the run. The $F$ and PSD parts of Figure 1 refer to the patterns across space of those phases and amplitudes at specific points in time. Taken together they give us an impression of $F$ and PSD as stochastic processes in time and, indeed, as evolving random fields.

Expectedly, the phase and amplitude patterns coincide. Amplitudes are large where the processes are approximately in phase, or synchronized. (Compare the phase pattern in the center panel with the one in Figure 3, which is similar to the starting pattern of the phases). This is even more apparent in the center panel of Figure 2. The pattern grows in amplitude in time, after an initial period of pattern formation.

The number of spatial cycles on the ring of amplitude processes is exactly twice the number produced for a similar but simpler neural field model (cf. (P. E. Greenwood & Ward, 2017)). This is true for various parameter sets inserted in (4.2) that produce a variety of different maximum values of the PSD of the MH operator. For example, Figure 2 shows a pattern resulting from MH parameters that would produce 7 spatial cycles in the simple neural field, but produces 14, or twice as many, in the quasi-cycle model. This is because each spatial cycle in phase results in two maxima in amplitude. The difference between the two models in number of spatial cycles of amplitude arises from the difference in the MH coupling: in the model studied in (P. E. Greenwood & Ward, 2017) there was no quasi-cycle rotation, and thus no phase involved in the coupling. In the present model, in (2.8) (2.9), the MH coupling of each pair of quasi-cycle amplitudes, $Z_j, Z_l$, is mediated by the cosine.
Figure 1. Upper panels: Phase and amplitude paths for 10,000 iterations of MH-coupled equations (2.8) (2.9) on a ring. Lower panels: F and PSD of the average over 500 iteration segments of the 128 MH-coupled amplitude components. Inset in center displays phases of the 128 components on the 10,000th iteration. Parameters were \( b_1 = 4, d_2 = 5, c = 0.4, \) noise SD = 0.5, \( Z_{\text{max}} = 5 \) and those in Table 1.

of the difference between their corresponding phases, \( \theta_j, \theta_l; C_{jl}Z_j \cos(\theta_j(t) - \theta_l(t)) \). Where these phases are more similar, typically near positive or negative peaks of the phase spatial cycle, the coupling of amplitudes is more effective, producing maxima of amplitude.

Note that in Figure 1 coupling strength \( c = 0.4 \), whereas in Figure 2 \( c = 3.9 \). The lower coupling strength is sufficient in the first example because the parameter values \( b_1 = 4, d_2 = 5 \) create a Mexican Hat operator whose maximum PSD exceeds a threshold for pattern creation in the present model. (The computation of this criterion is described in (Murray, 1989) for a simpler model). On the other hand, the maximum PSD of the Mexican Hat operator created by the values \( b_1 = 1.3, d_2 = 1.5 \) does not reach this threshold, and so the operator must be multiplied by a factor greater than 1 in order to exceed the pattern-creation threshold (cf. (P. E. Greenwood & Ward, 2017)). The value \( c = 3.9 \) in fact results in a MH operator that more than suffices to create pattern; it was chosen for clarity.

It will be noticed in Figures 1 and 2 that there are two dominant frequencies in the amplitude spatial pattern, somewhat mirrored in the phase pattern. The low
Figure 2. Upper panels: Phase and amplitude paths for 10,000 iterations of MH-coupled equations (2.8) (2.9) on a ring. Lower panels: F and PSD of the average over 500 iteration segments of the 128 MH-coupled amplitude components. Inset in center displays phases of the 128 components on the 10,000th iteration. Parameters were $b_1 = 1.3, d_2 = 1.5, c = 3.9, \text{noise SD} = 0.5, Z_{\text{max}} = 5$ and those in Table 1.

frequency reflects the fact that part of the higher frequency pattern is less developed, viz. the end components in Figure 1 and both middle and end components in Figure 2. The lower frequency is absent with higher values of $c$. This indicates that the lower frequency reflects the fact that the spatial pattern develops at different rates in different parts of the spatial array.

4.2. Reaction-coupling in one spatial dimension: system (3.19), (3.20). We ran simulations of (3.19), (3.20) using the same parameters as in Section 4.1. As expected, spatial patterns did not appear in the quasi-cycle phases, $\theta_j$ (upper left panel of Fig. 3). Instead the phases stayed as unsynchronized by the 10,000th iteration as they were at the beginning of the run (center inset in Fig. 3). This was expected because the BG factorization separates the rotation, with frequency $\omega$, from the stochastic neural field processes, as in (3.17), (3.18). The amplitudes, however, did display distinct spatial patterns. It was expected that these patterns would mirror those of the Mexican Hat-coupled neural field we studied in (P. E. Greenwood & Ward, 2017) and indeed this is the case (upper right panel of Fig. 3). The number of cycles exhibited in the stochastic path for the simulations
of (3.20) are exactly what would be predicted from Murray’s (Murray, 1989) treatment and our own (P. E. Greenwood & Ward, 2017). For the parameters used for Fig. 3 seven cycles are predicted and seven are observed.

**Figure 3.** Upper panels: Stochastic paths of the quasi-cycle phases and amplitudes from (3.19) and (3.20) Lower panels F and PSD of the average over 500 iteration segments of the 128 MH-coupled amplitude processes. Parameters were \( b_1 = 1.3, d_2 = 1.5, c = 1, \) noise SD = 1.0, \( Z_{\text{max}} = 5 \) and those in Table 1.

4.3. Reaction-coupling in two spatial dimensions: system (2.8), (2.9). We simulated processes (2.8) and (2.9) as in Section 4.1 on a 100x100 lattice (10,000 processes in all). The processes and the 2D Mexican Hat operator all had the same parameters as in the 1D case. We simulated the 10,000, locally-coupled (except for a boundary band 1/2 the width of the operator around the outside of the lattice), stochastic amplitude and phase processes for 1000 iterations and examined the spatial pattern of amplitudes and phases at various points during the runs. It should be emphasized again that all 10,000 processes were always oscillating in an approximately 70 Hz quasi-cycle during the entirety of each run. Thus, the spatial patterns we see occur in concert with oscillations in time. Figures 4, 5, and 6 display typical results at the end of the 1000 iterations. Clear spatial patterns appear in the amplitudes, comprising patches of higher amplitude arranged in stripes at spatial frequencies indicated in Figure 6. Spatial patterns also appear in the phases. These patterns comprise synchronized in-phase patches of stochastic
processes, oscillating at roughly 70 Hz, aligned in patches on the lattice but with adjacent patches roughly $\pi$ radians out of phase with each other. Raised and lowered patches in the amplitudes occur in corresponding locations in the lattice. We expect that two-dimensional simulations of (3.19), (3.20) will show amplitude bumps on patches but no phase synchronization, as in the one-dimensional case.

**Figure 4.** Average over the final one of 1000 iterations of the 10,000, 2D, MH-coupled amplitude processes. Parameters were $b_1 = 1.3$, $d_2 = 1.5$, $c = 4.7$, $\text{noise SD} = 0.5$, $Z_{max} = 5$ and those in Table 1.

**Figure 5.** Phase on the final one of 1000 iterations of the 10,000, 2D, MH-coupled phase processes. Parameters were $b_1 = 1.3$, $d_2 = 1.5$, $c = 4.7$, $\text{noise SD} = 0.5$, $Z_{max} = 5$ and those in Table 1.
5. Discussion

Global (Kuramoto) and local (Mexican Hat) couplings produce very different results for the evolution of the respective stochastic systems. In particular, sufficiently strong global coupling leads to widespread phase synchronization and roughly uniform amplitudes among the local systems (P. Greenwood et al., 2016), whereas sufficiently strong local coupling leads to an interesting spatial pattern of phase synchronization and also to a corresponding pattern of high and low amplitudes as in the present system (2.8), (2.9). In the system (3.19), (3.20), however, where the quasi-cycle rotations are not coupled, spatial patterns appear only in the amplitudes; the phases remain stochastically related to each other.

5.1. Mexican Hat coupling and amplitude explosions. Our simulations showed increases in amplitude, although, as we said, we worked in a parameter range, and in a time interval, where the threshold we set would have been attained only with small probability. In spite of the need to keep a stochastic neural field finite, a range of types of coupling can lead to inevitable increases in the amplitudes of the components. The function $G$ in (2.1) has the role of keeping the coupling term from overwhelming the reaction term (which is damping). Other simulations show that most choices of $G$, including the logistic and our own, can accomplish this when the coupling is relatively weak and applies only to a few neighbors. But if the coupling is extensive, e.g., an all-to-all coupling (as in (Daffertshofer & van Wijk, 2011)) or a large and steep Mexican Hat (present work), amplitudes can reach high values even in the presence of a limiting function $G$.

This fact suggests that in real neural systems the application of such couplings must be limited to transient responses, so that the neural field doesn’t saturate, at which point its functionality is compromised. Indeed this is the case in most neural systems (Barth & Poulet, 2012); although saturation does occur in some cases (e.g.,
very intense sensory stimuli) it is generally avoided, and firing rates of neurons are typically rather low and firing is sparsely distributed (e.g., (Barth & Poulet, 2012)). Exactly how this is accomplished is still uncertain, but apparently there are cortical mechanisms that promote sparseness (Barth & Poulet, 2012). Moreover, global inhibition tends to destroy synchronization (Terman & Wang, 1995) and decrease amplitude, so that, in the presence of certain input, development of a spatial pattern would be quenched for some time period. Intermittent application of global inhibition could encourage transient development of varied spatial patterns controlled by parameter values that change with stimulus or other input conditions. Such conditions could be simulated using our system (2.8), (2.9) along with a global inhibition operator and changing parameter values for the Mexican Hat operator as well as for the values of the synaptic efficacies in (4.1).

5.2. Mexican Hat coupling and noise smoothing in a generic stochastic neural field equation. In (P. E. Greenwood & Ward, 2017) we studied spatial patterns produced by Mexican Hat coupling of stochastic neural field equations with a simple reaction term in the context of the exposition by Murray (Murray, 1989). We found that when the solutions damped to a vanishingly small amplitude, even in the presence of excitable modes of the coupling that produced spatial patterns, added noise amplified, revealed, and sustained these patterns. Moreover, when we used spatially-smoothed noise, the smoothing itself produced spatial patterns that interacted with the patterns produced by Mexican Hat coupling. This result led us to expect that similar spatial patterns would be seen in the context of this more complicated stochastic neural field equation that implements a quasi-cycle oscillator as the reaction term. This has yet to be confirmed.

5.3. Comparison to other models. Our topic in this paper is Mexican Hat coupling of quasi-cycles. Numerous works in the literature, (Daffertshofer & van Wijk, 2011; Faugeras & Inglis, 2015; P. E. Greenwood & Ward, 2017; Heitman & Ermentrout, 2015; Murray, 1989), among others, describe studies of Mexican Hat coupling but none, to our knowledge, apply the coupling to quasi-cycles. Heitman and Ermentrout (Heitman & Ermentrout, 2015) modeled neural activity as a one-and two-dimensional ring of Mexican-hat-coupled phase oscillators, using Kuramoto equations. Their system is like our system (2.8), but with amplitude $Z = 1$ and no noise. Their analyses of stability suggest that their results on spatial patterns as a function of the extent of inhibition in the Mexican Hat operator might be extended to our setting.

In the work by Park et al. (Park, Heitman, & Ermentrout, 2017), in a similar setting, the notion of instantaneous phase response curve is carefully defined and used to derive phase-dynamic equations for coupled deterministic oscillators. Again, their results might well be extended to coupled quasi-cycles in a stochastic setting.

Appendix A. Details of Itô calculation for Equation (2.7)

Here we use Itô’s Lemma to express (2.7) in polar coordinates in order to obtain (2.8), (2.9) for the Mexican-Hat-coupled system. To do this, for clarity, we first use the simplest form of discrete approximation to the Laplacian operator, the double difference, in place of $M$. Then in Appendix B we derive (2.8), (2.9) from a more general form of (A.1), (A.2) that represents the Mexican Hat operator.
Writing (2.7) out explicitly for the \(j\)th stochastic process, where \(j\) is the index over the single, discretized, space dimension and the time index \(t\) is suppressed, we obtain

\[
(A.1) \quad du_j = (-\lambda u_j + \omega v_j)dt + (u_{j-1} - 2u_j + u_{j+1})dt + dW_j^u
\]

\[
(A.2) \quad dv_j = (-\omega u_j - \lambda v_j)dt + (v_{j-1} - 2v_j + v_{j+1})dt + dW_j^v
\]

Let \(u_j, v_j, j = 1, 2, \ldots, n\) be given by stochastic differential equations, such as (A.1), (A.2). Itô’s Lemma says that if \(f\) is a smooth function on \(\mathbb{R}^2\), then

\[
(A.3) \quad df\left(\begin{array}{c} u_j \\ v_j \end{array}\right) = (\nabla f)^\top\left(\begin{array}{c} u_j \\ v_j \end{array}\right) + \frac{1}{2} \left(\begin{array}{c} u_j \\ v_j \end{array}\right)^\top Hf\left(\begin{array}{c} u_j \\ v_j \end{array}\right),
\]

where

\[
\nabla f\left(\begin{array}{c} u_j \\ v_j \end{array}\right) = \left(\frac{\partial f}{\partial u_j}, \frac{\partial f}{\partial v_j}\right),
\]

and

\[
Hf\left(\begin{array}{c} u_j \\ v_j \end{array}\right) = \begin{bmatrix}
\frac{\partial^2 f}{\partial u_j^2} & \frac{\partial^2 f}{\partial u_j \partial v_j} \\
\frac{\partial^2 f}{\partial v_j \partial u_j} & \frac{\partial^2 f}{\partial v_j^2}
\end{bmatrix}.
\]

We wish to compute \(df\left(\begin{array}{c} u_j \\ v_j \end{array}\right)\) and \(dg\left(\begin{array}{c} u_j \\ v_j \end{array}\right)\), where

\[
Z_j = f\left(\begin{array}{c} u_j \\ v_j \end{array}\right) = (u_j^2 + v_j^2)^{\frac{3}{2}},
\]

and

\[
\theta_j = g\left(\begin{array}{c} u_j \\ v_j \end{array}\right) = \arctan\left(\frac{v_j}{u_j}\right),
\]

and where \(u_j, v_j\) are defined by (A.1), (A.2).

We begin by computing \(dZ_j\). We find that the gradient is

\[
\nabla Z_j\left(\begin{array}{c} u_j \\ v_j \end{array}\right) = \left(\frac{u_j}{Z_j}, \frac{v_j}{Z_j}\right),
\]

and the Hessian is

\[
HZ_j\left(\begin{array}{c} u_j \\ v_j \end{array}\right) = \frac{1}{Z_j^2} \left[I - \frac{1}{Z_j^2} \left(\begin{array}{cc} u_j^2 & u_jv_j \\ v_ju_j & v_j^2 \end{array}\right)\right].
\]

The first term on the RHS of (A.3) is

\[
(A.4) \quad \left(\nabla Z_j\right)^\top d\left(\begin{array}{c} u_j \\ v_j \end{array}\right) = \left(\begin{array}{c} u_j \\ v_j \end{array}\right)^\top \left(\begin{array}{c} u_j \\ v_j \end{array}\right)
\]

\[
= \frac{1}{Z_j}\left(-\lambda(u_j^2 + v_j^2) + M_j^Z\right)dt + dW_j
\]

\[
\overset{d}{=} \left(-\lambda Z_j + \frac{M_j^Z}{Z_j}\right)dt + dW_j,
\]
where
\[ M^Z_j = u_j u_{j-1} - 2u_j^2 + u_j u_{j+1} + v_j v_{j-1} - 2v_j^2 + v_j v_{j+1}. \]

The second term on the RHS of (A.3) is
\[ \frac{1}{2} d\left( \frac{u_j}{v_j} \right)^\top \left[ \frac{1}{Z_j} \left( I - \frac{1}{Z_j^2} \begin{pmatrix} u_j^2 & u_j v_j \\ u_j v_j & v_j^2 \end{pmatrix} \right) \right] d\left( \frac{u_j}{v_j} \right). \]

First consider the term of (A.8) containing \( I \), which gives
\[ \frac{1}{2Z_j}( (du_j)^2 + (dv_j)^2 ). \]

We use (A.1), (A.2), compute the squares, and obtain several terms. There are two terms containing \( (du_j)^2 \), \( (dv_j)^2 \), which we replace by \( dt \). All other terms are of lower order. Hence this term yields
\[ \frac{dt}{Z_j}. \]

Now consider the remaining term of (A.8). Again we use (A.1), (A.2) to evaluate \( du_j, dv_j \), and again \( (du_j)^2 = (dv_j)^2 = dt \). The other terms are all of lower order. The expression reduces to
\[ -\frac{1}{2Z_j^2} Z^2_j dt = -\frac{dt}{2Z_j}. \]

The two terms of (A.8) combine to give us
\[ \frac{dt}{2Z_j}. \]

Combining this with (A.4) we obtain
\[ dZ_j = \left[ \left( \frac{1}{2Z_j} - \lambda Z_j \right) + \frac{M^Z_j}{Z_j} \right] dt + dW_j. \]

Now we compute \( M^Z_j \) defined by (A.7) using
\[ u_j = Z_j \cos \theta_j, v_j = Z_j \sin \theta_j. \]

We obtain
\[ M^Z_j = Z_j Z_{j-1} (\cos \theta_j \cos \theta_{j-1} + \sin \theta_j \sin \theta_{j-1}) \]
\[ + Z_j Z_{j+1} (\cos \theta_j \cos \theta_{j+1} + \sin \theta_j \sin \theta_{j+1}) - 2Z_j^2 \]
\[ = Z_j Z_{j-1} \cos(\theta_j - \theta_{j-1}) + Z_j Z_{j+1} \cos(\theta_j - \theta_{j+1}) - 2Z_j^2. \]

With the above for \( M^Z_j \), (A.7) becomes
\[ dZ_j = \left( \frac{1}{2Z_j} - \lambda Z_j \right) dt \]
\[ + \left( Z_{j-1} \cos(\theta_j - \theta_{j-1}) + Z_{j+1} \cos(\theta_j - \theta_{j+1}) - 2Z_j \right) dt + dW_j. \]

The computation of the stochastic differential equation that defines the process \( \theta(u_j, v_j) = \arctan(v_j/u_j) \) goes similarly. First,
\[ (\nabla g)^\top = \left( \frac{u_j}{Z_j^2}, \frac{-v_j}{Z_j^2} \right). \]
Then
\[
(\nabla \theta_j)^\top d \begin{pmatrix} u_j \\ v_j \end{pmatrix} = \left( \begin{pmatrix} u_j & -v_j \\ \frac{Z_j}{Z_j^2} & \frac{Z_j}{Z_j^2} \end{pmatrix} d \begin{pmatrix} u_j \\ v_j \end{pmatrix}
\right)
\]
\[
= \frac{1}{Z_j^2} \left( v_j [-\lambda u_j + \omega v_j] - u_j [-\omega u_j - \lambda v_j] \right) dt + \frac{M^\theta_j dt}{Z_j^2} + dW_j
\]
\[
= \frac{1}{Z_j^2} (\omega v_j^2 + \omega u_j^2) dt + \frac{M^\theta_j dt}{Z_j^2} + dW_j
\]
\[
= \omega dt + \frac{M^\theta_j dt}{Z_j^2} + dW_j,
\]
where
\[
M^\theta_j = u_j u_{j-1} + u_j u_{j+1} - v_j v_{j-1} - v_j v_{j+1}.
\]
Computing \(M^\theta_j\) using the definitions of \(u_j, v_j\) as for \(M^Z_j\) we have
\[
\frac{M^\theta_j}{Z_j^2} = Z_{j-1} \sin(\theta_j - \theta_{j-1}) + Z_{j+1} \sin(\theta_j - \theta_{j+1}).
\]
The Hessian
\[
H\theta_j = \frac{1}{Z_j^2} \begin{pmatrix} -2u_j v_j & 1 - \frac{2u_j}{Z_j^2} \\ -1 + \frac{2u_j^2}{Z_j^2} & 2u_j v_j \end{pmatrix},
\]
so the Hessian term in (A.3) with \(f = \theta_j\) is
\[
\frac{1}{2} \frac{d}{Z_j^2} \left[ -2u_j v_j dt + 2u_j v_j dt + l.o.t. \right] \approx 0,
\]
and so the Hessian term does not contribute to \(d\theta_j\). Finally,
\[
d\theta_j = \omega dt + \frac{dW_j}{Z_j}
\]
\[
\approx \left( \frac{Z_{j-1}}{Z_j} \sin(\theta_j - \theta_{j-1}) + \frac{Z_{j+1}}{Z_j} \sin(\theta_j - \theta_{j+1}) \right) dt.
\]

**Appendix B. Extension to Mexican Hat operator for Equation (2.7)**

We introduce the simplest Mexican Hat operator possible, with the kernel extending over only 2 neighbors on each side of the process of interest. We will show that this kernel can be extended as far as is wished. Our two stochastic differential equations appear as
\[
a_j = (-\lambda u_j + \omega v_j) dt + (-u_{j-2} + u_{j-1} + u_j + u_{j+1} - u_{j+2}) dt + dW_j^u
\]
\[
\approx (-\omega u_j - \lambda v_j) dt + (-v_{j-2} + v_{j-1} + v_j + v_{j+1} - v_{j+2}) dt + dW_j^v.
\]
Again,
\[ Z_j = f \left( \frac{u_j}{v_j} \right) = (u_j^2 + v_j^2)^{\frac{1}{2}}, \]
and
\[ \theta_j = g \left( \frac{u_j}{v_j} \right) = \arctan \left( \frac{v_j}{u_j} \right). \]

Applying Itô’s Lemma as in Appendix A we have
\[
(\nabla Z_j)^\top d \left( \frac{u_j}{v_j} \right) = \left( \frac{u_j}{Z_j} - \frac{v_j}{Z_j} \right) dt + \frac{u_j}{Z_j} dW_j,
\]
\[
\left( [(-\lambda u_j + \omega v_j) + (-u_j - 2 + u_j - 1 + u_j + u_j + 1 - u_j + 2)] dt + dW^u_j \right)
\]
\[
\left( [(-\omega u_j - \lambda v_j) + (-v_j - 2 + v_j - 1 + v_j + v_j + 1 - v_j + 2)] dt + dW^v_j \right)
\]
\[
= \frac{1}{Z_j} \left( -\lambda (u_j^2 + v_j^2) + M_j^Z \right) dt + dW_j
\]
\[
= \left( -\lambda Z_j + \frac{M_j^Z}{Z_j} \right) dt + dW_j,
\]
as in Appendix A but where here
\[
M_j^Z = [u_j(-u_j - 2 + u_j - 1 + u_j + u_j + 1 - u_j + 2)
+ v_j(-v_j - 2 + v_j - 1 + v_j + v_j + 1 - v_j + 2)].
\]
The remainder of Itô’s Lemma gives the same results as in Appendix A for any \( du_j \) and \( dv_j \), so we have for the Mexican Hat coupling:
\[
dZ_j = \left( \frac{1}{2Z_j} - \lambda Z_j \right) dt + \frac{M_j^Z}{Z_j} dt + dW_j.
\]
Notice that (B.5) is only different from (A.9) in the form of \( M_j^Z \). This means that when we insert \( u_j = Z_j \cos \theta_j \) and \( v_j = Z_j \sin \theta_j \) into \( M_j^Z \) to obtain the final form, no matter what coupling we use, we just have to compute \( M_j^Z \) and then compute the result of the insertion, because only \( M_j^Z \) has \( u_j \) and \( v_j \) terms in it.

Now, inserting the polar coordinate expressions for \( u_j \) and \( v_j \) into (C.4), we have
\[
M_j^Z = -Z_j \cos \theta_j Z_j - 2 \cos \theta_j-2 + Z_j \cos \theta_j Z_j - 1 \cos \theta_j - 1 + (Z_j \cos \theta_j)^2
+ Z_j \cos \theta_j Z_j + 1 \cos \theta_j + 1 - Z_j \cos \theta_j Z_j + 2 \cos \theta_j + 2
- Z_j \sin \theta_j Z_j - 2 \sin \theta_j - 2 + Z_j \sin \theta_j Z_j - 1 \sin \theta_j - 1 + (Z_j \sin \theta_j)^2
+ Z_j \sin \theta_j Z_j + 1 \sin \theta_j + 1 - Z_j \sin \theta_j Z_j + 2 \sin \theta_j + 2.
\]
Collecting terms yields
\[
M_j^Z = Z_j \left[ -Z_j - 2 \cos(\theta_j - \theta_j - 2) + Z_j - 1 \cos(\theta_j - \theta_j - 1)
+ Z_j + 1 \cos(\theta_j - \theta_j + 1) - Z_j + 2 \cos(\theta_j - \theta_j + 2) + Z_j \right]
\]
\[
= Z_j \left[ \sum_{i=-N}^{N} C_{j,i} Z_{j+i} \cos(\theta_j - \theta_j + i) \right],
\]
where \( C_{j,i} \) represents the coefficients of the Mexican Hat operator; here we have taken them to be +1 or -1 to establish the pattern. \( N = 2 \) in our derivation but
could be larger, involving more negative and positive terms, widening the operator. The coefficients of the terms in the Mexican Hat operator could be any real numbers as they are in the difference-of-Gaussians operator we use in this paper, and could also implement an asymmetric operator. Finally, the entire operator can be modulated by multiplication of its coefficients by some number to represent coupling strength. We do this in our simulations.

The final expression for the approximation with the just-derived coupling becomes

\[(B.6) \quad dZ_j = \left(\frac{1}{2Z_j} - \lambda Z_j\right)dt + \left(\sum_{i=-N}^{N} C_{j,j+i} Z_{j+i} \cos(\theta_j - \theta_{j+i})\right)dt + dW_j,\]

The derivation of the more general form for \(d\theta_j\) proceeds in the same fashion, with the result that

\[(B.7) \quad d\theta_j = \omega dt + \left(\sum_{i=-N}^{N} C_{j,j+i} \frac{Z_{j+i}}{Z_j} \sin(\theta_j - \theta_{j+i})\right)dt + \frac{dW_j}{Z_j}.\]

**Appendix C. Details of Itô calculation for Equation (3.17)**

Again we apply the simplest Mexican Hat operator possible, with the kernel extending over only 2 neighbors on each side of the process of interest, as in Appendix B. Here our two stochastic differential equations appear as

\[(C.1) \quad du_j = -u_j dt + (-u_{j-2} + u_{j-1} + u_j + u_{j+1} - u_{j+2}) dt + dW^u_j,\]

\[(C.2) \quad dv_j = -v_j dt + (-v_{j-2} + v_{j-1} + v_j + v_{j+1} - v_{j+2}) dt + dW^v_j.\]

Note, however, that here the stochastic differential equations do not contain the rotation. Again,

\[Z_j = f\left(\frac{u_j}{v_j}\right) = (u_j^2 + v_j^2)^{\frac{1}{2}},\]

and

\[\phi_j = g\left(\frac{u_j}{v_j}\right) = \arctan\left(\frac{v_j}{u_j}\right),\]

where we have changed the notation of the phase to indicate that it is now stochastic phase rather than the phase of a stochastic rotation. Applying Itô’s Lemma as in Appendix B we have

\[(\nabla Z_j)^\top d\left(\frac{u_j}{v_j}\right) = \left(\frac{u_j}{Z_j}, \frac{v_j}{Z_j}\right)\]

\[\left([-u_j + (-u_{j-2} + u_{j-1} + u_j + u_{j+1} - u_{j+2})]dt + dW^u_j\right)\]

\[\left([-v_j + (-v_{j-2} + v_{j-1} + v_j + v_{j+1} - v_{j+2})]dt + dW^v_j\right)\]

\[(C.3) \quad = \frac{1}{Z_j^2}(-u_j^2 - u_{j-2}u_{j-1} + u_j^2 + u_{j+1} - u_{j+2})dt + u_j dW^u_j\]

\[+ \frac{1}{Z_j^2}(-v_j^2 - v_{j-2}v_{j-1} + v_j^2 + v_{j+1} - v_{j+2})dt + v_j dW^v_j\]

\[\equiv d\left(-Z_j + \frac{M^2_j}{Z_j}\right)dt + dW_j,\]
as in Appendix B but where here

\begin{equation}
M_j^Z = \left[u_j(-u_{j-2} + u_{j-1} + u_j + u_{j+1} - u_{j+2})
+ v_j(-v_{j-2} + v_{j-1} + v_j + v_{j+1} - v_{j+2})\right].
\end{equation}

(C.4)

The remainder of Itô’s Lemma gives the same results as in Appendix B for any \(du_j\) and \(dv_j\), so we have for the Mexican Hat coupling:

\begin{equation}
dZ_j = \left(\frac{1}{2Z_j} - Z_j\right)dt + \frac{M_j^Z}{Z_j}dt + dW_j.
\end{equation}

(C.5)

Notice that (C.5) is only different from (B.5) in the form of \(M_j^Z\). This means that when we insert \(u_j = Z_j \cos \phi_j\) and \(v_j = Z_j \sin \phi_j\) into \(M_j^Z\) to obtain the final form, no matter what coupling we use, we just have to compute \(M_j^Z\) and then compute the result of the insertion, because only \(M_j^Z\) has \(u_j\) and \(v_j\) terms in it.

Now, inserting the polar coordinate expressions for \(u_j\) and \(v_j\) into (C.4), we have

\begin{align*}
M_j^Z &= -Z_j \cos \phi_j Z_{j-2} \cos \phi_{j-2} + Z_j \cos \phi_j Z_{j-1} \cos \phi_{j-1} + (Z_j \cos \phi_j)^2 \\
&\quad + Z_j \cos \phi_j Z_{j+1} \cos \phi_{j+1} - Z_j \cos \phi_j Z_{j+2} \cos \phi_{j+2} \\
&\quad - Z_j \sin \phi_j Z_{j-2} \sin \phi_{j-2} + Z_j \sin \phi_j Z_{j-1} \sin \phi_{j-1} + (Z_j \sin \phi_j)^2 \\
&\quad + Z_j \sin \phi_j Z_{j+1} \sin \phi_{j+1} - Z_j \sin \phi_j Z_{j+2} \sin \phi_{j+2}.
\end{align*}

Collecting terms yields

\begin{align*}
M_j^Z &= Z_j \left[ - Z_{j-2} \cos(\phi_j - \phi_{j-2}) + Z_{j-1} \cos(\phi_j - \phi_{j-1}) \\
&\quad + Z_{j+1} \cos(\phi_j - \phi_{j+1}) - Z_{j+2} \cos(\phi_j - \phi_{j+2}) + Z_j \right] \\
&= Z_j \left[ \sum_{i=-N}^{N} Z_{j+i} \cos(\phi_j - \phi_{j+i}) \right].
\end{align*}

The final expression for the approximation with the just-derived coupling becomes

\begin{equation}
dZ_j = \left(\frac{1}{2Z_j} - Z_j\right)dt + \left(\sum_{i=-N}^{N} C_{j,j+i} Z_{j+i} \cos(\phi_j - \phi_{j+i})\right)dt + dW_j,
\end{equation}

(C.6)

where, again, \(C_{j,j+i}\) represents the coefficients of the Mexican Hat operator, with the same possible values, as in Appendix B.

The derivation of the more general form for \(d\phi_j\) proceeds in the same fashion, with the result that

\begin{equation}
d\phi_j = \frac{dW_j}{Z_j} + \left(\sum_{i=-N}^{N} C_{j,j+i} \frac{Z_{j+i}}{Z_j} \sin(\phi_j - \phi_{j+i})\right)dt.
\end{equation}

(C.7)

Notice that here that the Mexican Hat coupling is modified by the difference between the stochastic phases, \(\phi_j\), which are random, so that this form introduces noise into the coupling rather than coupling the quasi-cycle oscillations.

**Competing interests**

The authors declare that they have no competing interests.
Author’s contributions

Both authors contributed to the conceptualization and writing of the paper. The numerical simulations were accomplished by LMW.

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