Cusps Enable Line Attractors for Neural Computation

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INTRODUCTION

Attractor neural networks have been appealed to by theoretical neuroscientists to explain working memory, oculomotor control, head movement, locomotion, and sensory processing. Some of these neuronal functions have been rationalized using the persistent activity of an attractor (e.g., working memory), while other functions have been modeled by the gradedness (i.e., order preserving property) of an attractor (e.g., oculomotor control and sensory processing). Because of these dynamical features, attractor networks have been particularly useful in modeling the encoding of continuous external stimuli or the maintenance of internal neuronal representations. Furthermore, it has been shown that attractor network dynamics have the capacity to perform optimal computations and thus, can implement Bayesian inference.

Pulse-gating is a mechanism capable of transferring packet-based spiking activity from one neuronal population to another. For instance, the synfire-gated synfire chain (SGSC) is a mechanism consisting of two sets of neural populations, one representing rate-coded (graded) information and another that gates the flow of that information. This separation into information-carrying and information-control populations provides a basis for understanding how some brain areas can be responsible for the control of information transfer, such as the mediodorsal nucleus of the thalamus and others for information processing, such as the somatosensory areas.

The original information propagation model that demonstrated the concept of pulse-gated firing rate propagation was based on a mean-field firing rate model of a network of current-based integrate-and-fire (I&F) neurons that was coarse-grained in time. There was good correspondence between the mean-field model and mean spiking rates in a network of I&F neurons. However, in general, mean-field models make critical use of f-I curves (or other input-output functions), which correspond to the steady-state responses of a population of neurons driven by a constant input. There is no a priori reason that a temporally-averaged mean-field model should correspond with an I&F network in a transiently driven (pulse-gating) context. Furthermore, the original mean-field solution that demonstrated pulse-gated information propagation suffered from parameter fine-tuning, even though I&F simulations appeared robust to parameter variability.

In this paper, in order to better understand the robustness of pulse-gated, graded information transfer in a network of spiking neurons, we construct Fokker-Planck equations describing the membrane potential probability density function...
tion in a feedforward network and study solutions in the state space of a dimensionally-reduced iterative dynamical system. After outlining our methods, we show that pulse-gating in feedforward networks gives rise to approximately time-translationally-invariant spiking probabilities that are propagated from layer to layer in a feedforward network. We then examine synaptic current input-output relations allowing for the construction of an effective population firing rate model and show that this model, averaged across neuronal populations, is very similar to a mean-field model based on rectified linear input-output functions. We show how the input-output function depends on synaptic coupling, gating pulse amplitude, and synaptic noise, and that there is a sizeable region of parameter space within which graded propagation exists.

We then demonstrate the dynamical convergence of membrane potential density to a one-dimensional manifold in parameter space. The Fokker-Planck system reveals that this one-dimensional manifold arises due to a saddle node bifurcation creating an unstable fixed point in the center of a linear manifold and two stable fixed points on either side of the saddle node. Dynamics orthogonal to the linear manifold give rise to rapid convergence to the linear manifold. Ghost (slow) dynamics along the one-dimensional manifold allow the unstable manifold of the saddle to be viewed as an attracting one-dimensional manifold.

We finally show that this approximate line attractor is robust and generic. By using a reduced analytical model of gating induced transients in the Fokker-Planck system, we show that the propagation of firing amplitudes can be mapped to a cusp catastrophe, and that a bundle of one-dimensional ghost manifolds exists in the region surrounding the fold of the cusp. Our results reveal how the coordination of pulse-gating, synaptic coupling, and membrane potential dynamics enables approximate line attractors in feedforward networks and demonstrate the robustness of graded information propagation when pulse-gating is incorporated.

**METHODS**

We study a feedforward network of \( j = 1, \ldots, M \) populations of \( i = 1, \ldots, N \) excitatory, current-based, integrate-and-fire (I&F) neurons whose membrane potential, \( V \), and synaptic current are described by

\[
\frac{d}{dt} V_{i,j} = -g_L(V_{i,j} - V_R) + I^S_{i,j} + I^H_{i,j} \quad (1a)
\]

\[
\tau \frac{d}{dt} I^H_{i,j} = -I^H_{i,j} - \frac{p}{2} \sum_k p_{jk} \sum_l \delta(t - t_{j-1,l}) - D_j \frac{\partial}{\partial V} \rho_j(V,t) \quad (1b)
\]

where \( V_R \) is the rest voltage (also the reset voltage), \( \tau \) is the synaptic timescale, \( S \) is the synaptic coupling strength, \( p_{jk} \) is a Bernoulli distributed random variable and \( p = \langle p_{jk} \rangle \) is the mean synaptic coupling probability. The \( j \)th spike time of the \( k \)th neuron in layer \( j-1 \) is determined by \( V_{i,j}(t_{j-1,k}) = V_{Th} \), i.e. when the neuron reaches threshold (after which \( V_{i,j} \) is immediately reset to \( V_R \)). The gating current, \( I^H_{i,j} \), is a white noise process with a square pulse envelope, \( \theta(t - (j - 1)T) - \theta(t - jT) \), where \( \theta \) is a Heaviside theta function and \( T \) is the pulse length of pulse height \( \bar{I}^S \) and variance \( \sigma^2_0 \). Note that an exponentially decaying current is injected in population 1 providing synchronized activity that will subsequently propagate downstream through populations \( j = 2, \ldots, M \).

Feedforward networks of this type admit discrete-time-translationally-invariant solutions describing graded packet transfer \([11] [12]\). Such solutions exist for gating pulses that are either temporally sequential or overlapping \([12]\).

To understand this phenomenon, we used a Fokker-Planck analysis. Assuming the spike trains in Eq. \([15]\) to be Poisson distributed, the collective behavior of this feedforward network may be described by the (Fokker-Planck) equations

\[
\frac{\partial}{\partial t} \rho_j(V,t) = -\frac{\partial}{\partial V} J_j(V,t) \quad (2a)
\]

\[
\tau \frac{d}{dt} J_j = -J_j + \left\{ \begin{array}{ll}
S m_{j-1}, & j > 1 \\
A \delta(t), & j = 1
\end{array} \right. \quad (2b)
\]

These equations describe the evolution of the probability density function, \( \rho_j(V,t) \), in terms of the probability density flux, \( J_j(V,t) \), the mean feedforward synaptic current, \( \bar{I}^S_j \), and the population firing rate, \( m_j \). For each layer, \( j \), the probability density function gives the probability of finding a neuron with membrane potential \( V \in (-\infty, V_{Th}] \) at time \( t \).

The probability density flux is given by

\[
J_j(V,t) = \left( -g_L(V - V_R) + \bar{I}^S_j + \bar{I}^H_j \right) - D_j \frac{\partial}{\partial V} \rho_j(V,t)
\]

The effective diffusivity is

\[
D_j = A^2_0 + \frac{1}{2} \frac{S^2}{pN} m_{j-1}(t).
\]

(Below, we take \( N \to \infty \) and neglect the second term on the right in \([3]\).) The population firing rate is the flux of the probability density function at threshold,

\[
m_j(t) = J_j(V_{Th},t) \quad (4)
\]

The boundary conditions for the Fokker-Planck equations are

\[
J_j(V_R^+,t) = J_j(V_{Th},t) + J_j(V_R^-,t), \quad \rho_j(V_R^+,t) = \rho_j(V_{Th},t) + \rho_j(V_R^-,t), \quad \text{and} \quad \rho_j(V = -\infty,t) = 0.
\]

To improve the efficiency of exploring the bifurcation structure of this system in a large state space, we also investigate an approximate model in which the initial distribution is assumed to be Gaussian, \( \rho_0(V,t) = (1/P) \exp(-\frac{(V - \mu(t))^2}{2\sigma^2}) \), with width \( \sigma \) and mean \( \mu(t) \), where \( P = \int_{-\infty}^{V_{Th}} \rho_0(V,0) \) is a normalization factor accounting for the truncation of the Gaussian at threshold, \( V_{Th} \). As the gating current turns on, the distribution is uniformly advected toward the voltage threshold, \( V_{Th} \), and the population begins to fire. Uniform advection neglects a small amount of firing due to a diffusive flux across the firing threshold, thus the fold bifurcation (see Results) occurs at a slightly larger value of synaptic coupling, \( S \), for this approximation relative to numerical simulations. Since the timescale of the
A) Graded population density transfer. Population densities in upstream, $\rho_u(V,t)$, and downstream, $\rho_d(V,t)$, layers. These are two layers from a 19 layer feedforward network with $T = 5$ ms, $S = 2.83$, $I_{\text{gate}} = 14.2$, and $\sigma_0 = 4.5$. B) Synaptic current, $I^g$ (blue), and firing rate, $m_i(t)$ (magenta), in upstream and downstream layers. Inset shows a comparison of a mean-field firing rate model (dashed red) with the population-averaged Fokker-Planck model (blue). Below the plot, we show the timing of the gating pulses. C) Graded firing rates showing faithful, pulse-gated propagation across 19 layers. The sets of successive blue traces (six amplitudes from bottom to top) are currents from each population. Gradedness is shown by the fact that the pulses retain their height (roughly) and order as they propagate from population to population. Gating pulses for the solutions depicted are shown at the bottom of each panel.

FIG. 1. Graded, pulse-gated propagation in a neural Fokker-Planck model. A) Graded population density transfer. Population densities in upstream, $\rho_u(V,t)$, and downstream, $\rho_d(V,t)$, layers. These are two layers from a 19 layer feedforward network with $T = 5$ ms, $S = 2.83$, $I_{\text{gate}} = 14.2$, and $\sigma_0 = 4.5$. B) Synaptic current, $I^g$ (blue), and firing rate, $m_i(t)$ (magenta), in upstream and downstream layers. Inset shows a comparison of a mean-field firing rate model (dashed red) with the population-averaged Fokker-Planck model (blue). Below the plot, we show the timing of the gating pulses. C) Graded firing rates showing faithful, pulse-gated propagation across 19 layers. The sets of successive blue traces (six amplitudes from bottom to top) are currents from each population. Gradedness is shown by the fact that the pulses retain their height (roughly) and order as they propagate from population to population. Gating pulses for the solutions depicted are shown at the bottom of each panel.

RESULTS

In Fig. 1, we show that population density (Fig. 1A), and graded current and firing rate (Fig. 1B) may be propagated via pulse-gating between layers in the Fokker-Planck model. In Fig. 1B inset, we compare currents between a time-averaged firing rate model of pulse-gated graded information propagation and the Fokker-Planck model. For a given value of $T$ in a mean-field rate model, we can find an exact $S$. Because of the slow onset of firing (blue, inset) relative to the firing rate model (dashed red, inset), the value of synaptic coupling that gave rise to graded transfer, $S = S_{\text{graded}}$, was larger than the mean-field prediction, $S_{\text{exact}}$ (see Appendix), by a factor of 1.07 for $T$ near 5 ms. In Fig. 1C, we demonstrate stable graded propagation across many layers.

In Fig. 2A,B, we show firing rates and corresponding current amplitudes for a range of input currents in the Fokker-Planck model. For all but the lowest input current, the output current (the current at the end of the gating pulse) is very close to the input current. Plotting input versus output current for ranges of gating currents, $I^g$ (Fig. 2C), and synaptic couplings, $S$ (Fig. 2D), we find that changes in gating currents translate the input-output function upwards and changes in synaptic coupling change the slope of the input-output function. By varying $I^g$ and $S$, we can find an optimal input-output function very close to the diagonal (Fig. 2E), hence giving very accurate propagation of graded information. A nearby basin of parameters also gives good graded propagation (Fig. 2F) as measured by the distance pulse is fast, neurons only have enough time to fire once (approximately). Thus, we neglect the re-emergent population at $V_R$, which contributes negligibly to firing during the transient pulse.

With this approximation, Eq. (2a) gives rise to $\dot{\mu} = -g_L(\mu - V_R) + I^g + \bar{I}^u$, where $\sigma^2 = \sigma_0^2/g_L$. With upstream current $\bar{I}^u = Ae^{-t/\tau}$. Setting $V_{\text{Th}} = 1$, this integrates to

$$\mu(t) = \mu_0 e^{-g_L t} + \bar{I}^g g_L (1 - e^{-g_L t}) + \frac{A}{\tau} e^{-(g_L t - e^{-t/\tau})}$$

and from Eq. (4), we have

$$m(t) = \left[\left(-g_L \mu(t) + \bar{I}^g + A e^{-t/\tau}\right) e^{-\left((1 - \mu(t))^2/2\sigma^2\right)}\right]^+,$$

which, from Eq. (2b), results in a downstream synaptic current at $t = T$

$$I^d = S e^{-T/\tau} \int_0^T e^{t/\tau} m(t) \frac{dt}{\tau}.$$  

After the end of the pulse, the current decays exponentially. This decaying current feeds forward and is integrated by the next layer. Thus, for an exact transfer, $I^d(S, \bar{I}^g, A, T) = A.$
close to the value of the synaptic input current. For (A) and (B),
of the gating pulse, indicated by the vertical red line, is very
tic input currents. Note that the peak of the current at the end
rents. B) Downstream currents plotted for given upstream synap-
stream firing rates plotted for given upstream synaptic input cur-
FIG. 2. Current transfer in the Fokker-Planck model. A) Down-
fer functions,
I
diagonal. The broad, roughly linear, range of gating currents, ¯
puts. F) The distance of the current transfer function from the
function closely approaches the diagonal over a large range of in-
fer function, with
S
slope of the input-output function. E) An optimal current trans-
S
transfer functions for three values of the synaptic coupling,
S
networks are impractical.
may be faithfully propagated.
vertical line appearing at the end of the gating pulse, indicated by the vertical red line, is highly close to the value of the synaptic input current. For (A) and (B),
stream currents plotted for given upstream synaptic input currents. Note that the peak of the current at the end of the gating pulse, indicated by the vertical red line, is very close to the value of the synaptic input current. For (A) and (B),
stream firing rates plotted for given upstream synaptic input currents. Note that the peak of the current at the end of the gating pulse, indicated by the vertical red line, is very close to the value of the synaptic input current. For (A) and (B),
stream currents plotted for given upstream synaptic input currents. Note that the peak of the current at the end of the gating pulse, indicated by the vertical red line, is very close to the value of the synaptic input current.
FIG. 3. The slow manifold of graded propagation. A) Trajectories, $(m_j(jT), M_1^j(jT), M_2^j(jT))$ for successive values of $j$, showing the rapid approach of the initial distribution to a one-dimensional manifold and the slow evolution along the manifold representing the slow decay of the waveform. The trajectories are plotted as red lines with blue arrows at the tip. Small blue tips along the one-dimensional manifold show the slow evolution. B) The trajectories in A) projected onto the $M_1 - m$ plane. In this panel, the black dots indicate the three fixed points on the one-dimensional manifold (outer fixed points stable, middle fixed point unstable). C) The trajectories in A) projected onto the $M_1 - M_2$ plane. Parameters are as in Fig. 1.

**DISCUSSION**

To understand pulse-gated information propagation, we used a Fokker-Planck analysis to derive input-output curves that may be used in population firing rate models of pulse-gated propagation and to reveal an approximate line attractor in the network of spiking neurons. We further showed that the line attractor is associated with ghost dynamics occurring along the front fold (relatively small synaptic coupling) of a cusp catastrophe as $\sigma$ varies in state space. Locally, the nearly one-dimensional attracting manifold is the result of a fold bifurcation where the stable directions of the saddle and attracting fixed points are strongly attracting and the unstable manifold exhibits ghost dynamics. In terms of input-output functions, this reflects that the fold of this cusp separates a region of sigmoidal f-I curves, with a relatively large linear interval, from a region of bistability. Since this region occupies a sizeable volume in parameter space, the graded propagation is robust. Furthermore, the fact that a common cusp catastrophe underlies the fast timescale dynamics of our system indicates that this type of line attractor is generic and will persist in feedforward networks of other types of spiking neurons.

One of the major problems of neuroscience is to understand how complex neural functions emerge from the collective dynamics of neuronal networks. Towards this goal, researchers have tried to construct models using mean-field firing rate theories and large-scale numerical simulations. However, except for a few examples (e.g. [19–21]), the precise correspondence between the underlying microscopic spiking neurons and the macroscopic coherent dynamics of the neuronal populations has not been established.

Our analysis provides a significant step toward understanding how macroscopic attracting manifolds can emerge from the dynamic interactions of microscopic spiking neurons via the coordination of pulse-gating, synaptic weights, and intrinsic and extrinsic noise (i.e. the distribution of the membrane potential across the population), and offers possible order parameters for which macroscopic descriptions can be derived from the underlying microscopic dynamical model.

Furthermore, transfer mechanisms, such as those found in the graded and binary transfer parameter regimes shown in Fig. 5. (i.e. for $S$ near the fold (graded) or $S$ to the right of the fold (binary)), provide a novel means of understanding dynamic network interactions such as the detailed measurements of population activity underlying complex neural tasks provided by modern experimental techniques. Already, pulse-gated transfer mechanisms have been shown to be capable of implementing dynamic modules representing complex neural functions, such as short term memory, decision...
and of obvious cusp catastrophe that occurs along the many layers. Models in parameter space that allow graded propagation across ghosts. Ghosts occur near the cusp locus producing a bundle of fixed points. For ward stable fixed points (either upward above the unstable fixed background, where the color indicates the speed of departure toward stable fixed points of the map of the synaptic feed forward current generated from Eqs. \[ S = \frac{\tau}{T} e^{t/T} \] we get exact, graded propagation, where the mean synaptic current and firing rates were

\[
I_j^{ff}(t) = \begin{cases} 
A \left( \frac{t-(j-1)T}{\tau} \right) e^{-\frac{(t-(j-1)T)}{\tau}}, & (j-1)T \leq t \leq jT \\
A \left( \frac{T}{\tau} e^{-T/T} \right) e^{-\frac{(T-jT)}{\tau}}, & jT < t < \infty
\end{cases}
\]

and

\[
m_j(t) = \begin{cases} 
0, & 0 < t < (j-1)T \\
A \left( \frac{T}{\tau} e^{-T/T} \right) e^{-\frac{(T-jT)}{\tau}}, & (j-1)T \leq t \leq jT \\
0, & jT < t < \infty
\end{cases}
\]

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APPENDIX: MEAN FIELD MODEL

A mean-field firing rate model of Eq. (1) is given by

\[
\frac{dI_j^{ff}}{dt} = -I_j^{ff} + Sm_{j-1}
\]

where \([\cdot]^+\) denotes a thresholded linear function, with threshold \(g_0\), for the input-output relation of an I&F neuron.

In [11], we showed that when the gating pulse cancels the threshold \((I_j = g_0)\), and the feedforward synaptic coupling strength was

\[
S_{exact} = \frac{\tau}{T} e^{T/T}
\]

FIG. 5. \(\sigma\)-induced fold bifurcation ghost at cusp catastrophe. A) The probability density as a function of time and membrane potential from a numerical simulation. B) The probability density as a function of time from the transient pulse approximation. C) A plot of the surface of zeros of \(I^3(S, I^5, A, \sigma) - A\) plotted for \((S, I^5, A)\) with \(\sigma = 0.2\). These are fixed points of the map of the synaptic fold bifurcation across many values of \(I^5\), similar to that found numerically in Fig. 3. D) A plot of the surface of zeros of \(I^3(S, I^5, A, \sigma) - A\) plotted for \((S, A, \sigma)\) with \(I^5 = 6.5\). Note the obvious cusp catastrophe that occurs along the \(A\)-axis. E) Zeros of \(I^3(S, I^5, A, \sigma) - A\) for \(I^5 = 6.5\) and \(\sigma = 0.2\) plotted on a colored background, where the color indicates the speed of departure toward stable fixed points (either upward above the unstable fixed point or downward below the unstable fixed point). For small \(\sigma\), solutions rapidly approach the fixed points, giving a propagated binary code for large \(S\). F) Zeros of \(I^3(S, I^5, A, \sigma) - A\) for \(I^5 = 6.5\) and \(\sigma = 1.0\) again indicating the speed of departure toward stable fixed points. For \(\sigma\) near the cusp, there is a large region within which propagation away from the unstable point is slow, called a ghost. Ghosts occur near the cusp locus producing a bundle of models in parameter space that allow graded propagation across many layers.
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