Neuronal connection efficacy exhibits two forms of short-term plasticity, namely, short-term depression (STD) and short-term facilitation (STF). They have time constants residing between fast neural signaling and slow learning, and may serve as substrates for neural systems manipulating temporal information in relevant time scales. The present study investigates the impact of STD and STF on the dynamics of continuous attractor neural networks (CANNs) and their potential roles in neural information processing. We find that STD increases the mobility of the network states. The increased mobility enhances the tracking performance of the network in response to time-varying stimuli, leading to anticipative neural responses. Furthermore, we find that STD endows the network with slow-decaying plateau behaviors, namely, the network being initially stimulated to an active state decays to silence very slowly in the time scale of STD rather than that of neural signaling. This provides a mechanism for neural systems to hold short-term memory easily and shut off persistent activities naturally. With STF, we find that the network can hold a memory trace of external inputs in the facilitated neuronal interactions, which provides a way to stabilize the network response to noisy inputs, leading to improved population decoding performances. In general, we find that STD and STF tend to have opposite effects on network dynamics and complementary computational advantages, suggesting that the brain may employ a strategy of weighting them differentially for serving different computational purposes.

Introduction

Experimental data has consistently revealed that the neuronal connection weight, which models the efficacy of the firing of a pre-synaptic neuron on modulating the state of a post-synaptic one, varies in short time scales, ranging from hundreds to thousands of milliseconds (see, e.g., [1,2,3,4]). This is called short-term plasticity (STP). Two types of STP, which have opposite effects on modifying the connection efficacy, have been observed, namely, short-term depression (STD) and short-term facilitation (STF). The biological process underlying STD is the depletion of available resources when neurotransmitters are released from the axon terminal of the pre-synaptic neuron during signal transmission [1,2,5]. For STF, the underlying cause is the elevated calcium residue after spike generation, which increases the releasing probability of neurotransmitters. So, is STP merely a by-product of the biological process associated with neural signaling? Computational studies on the impact of STP on network dynamics have strongly suggested that this is unlikely to be the case. Instead, STP can play many important roles in neural computation. For instance, cortical neurons receive pre-synaptic firing rates ranging from less than 1 to more than 200 hertz. It was suggested that STD provides a dynamic gain control mechanism that allows equal fractional changes on rapidly and slowly firing afferent to produce post-synaptic responses, realizing the Weber’s law [6,7]. Besides, computations can be performed in recurrent networks by population spikes in response to external inputs, which are enabled by STD by recurrent connections [8,9]. Another role played by synaptic depression was proposed in [10]. In neuronal systems, critical avalanches are believed to bring about optimal computational capabilities, and are observed experimentally. Synaptic depression enables a feedback mechanism so that the system can be maintained at a critical state, making the self-organized critical behavior robust [10]. Herding, a computational algorithm reminiscent of the neuronal dynamics with synaptic depression, is recently found to have a similar effect on the complexity of information processing [11]. Recently, STP is also thought to play a role for a neuron estimating the membrane potential information of the pre-synaptic neuron based on spikes it receives [12].

Concerning the computational significance of STF, a recent work proposed an interesting idea for achieving working memory in the prefrontal cortex [13]. The residual calcium of STF is used as a buffer to facilitate synaptic connections, so that inputs in a subsequent delay period can retrieve the information encoded by the facilitated synaptic connections. The STF-based memory mechanism has an advantage of not having to rely on persistent neural firing during the period that the working memory is functioning, and hence is energetically more efficient.

From the computational point of view, the time scale of STP resides between fast neural signaling (in the order of milliseconds) and slow learning (in the order of minutes or above), which is the time scale of many important temporal processes occurred in our daily life, such as the passive holding of a temporal memory of objects coming into our visual field (the so-called iconic sensory memory), or the active use of the memory trace of recent events for motion control. Thus, STP may serve as a substrate for neural systems manipulating temporal information in the relevant time scales. STP has been observed in many parts of the cortex, and also exhibits large diversity in different cortical areas, suggesting that the brain may employ a strategy of weighting STD and STF differently for serving different computational purposes.

In the present study, we explore the potential roles of STP in processing information derived from external stimuli, an issue of fundamental importance but has not been adequately investigated so far. For the convenience of describing our ideas, we use continuous attractor neural networks (CANNs) as the working models, but our main results are

**Reserved for Publication Footnotes**
qualitatively applicable to general cases. CANNs are recurrent networks which can hold a continuous family of localized active states [14]. Neutral stability is a key property of CANNs, which enables neural systems to update memory states easily and to track time-varying stimuli smoothly. CANNs have been successfully applied to describe the generation of persistent neural activities [15], the encoding of continuous stimuli, such as the orientation, the head direction and the spatial location of objects [16, 17, 15], and a framework for implementing efficient population decoding [19].

When STF is included in a CANN, the dynamics of the network is governed by two time scales. The time constant of STF is much larger than that of neural signaling, with the former and latter being of the order of $10^2 - 10^3$ ms and $10^0 - 10^1$ ms respectively. The interplay between the fast and the slow dynamics causes the network to exhibit rich dynamical behaviors, laying the foundation for the neural system to implement complicated functions.

In CANNs with STD, various network stationary activities have been reported, including damped oscillations [20], periodic and aperiodic dynamics [20], state hopping with transient population spikes [21], traveling fronts and pulses [22, 23, 24, 25], breathers and pulse-emitting breathers [23, 24], spiral waves [26], and rotating bump states [27]. Here, we focus on those network states relevant to the processing of stimulus in CANNs, including static, moving and metastatic states [14]. More significantly, we find that with STD, the network state can display slow-decaying plateau bumps [28, 29, 30, 31]. More significantly, we find that with stimulus in CANNs, including static, moving and metastatic dynamics causes the network to exhibit rich dynamical behaviors respectively. The interplay between the fast and the slow of STF, the network response is determined not only by the specific facilitation lasts in the time scale of STF, and it progressively increases the tracking speed of a CANN. Interestingly, for strong positive contributions in different computational tasks. Enhanced stability mediated by STF can improve the computational and behavioral stability of CANNs. To demonstrate that enhanced mobility can have a positive role in information processing, we investigate a computational task in which the network tracks time-varying stimuli. We find that STD increases the tracking speed of a CANN. Interestingly, for strong STD, the network state can even overtake the moving stimulus, reminiscent of the phase precessing behavior of place cells in the hippocampus [32, 35].

The Model
We consider a one-dimensional continuous stimulus $x$ encoded by an ensemble of neurons. For example, the stimulus may represent a moving direction, an orientation or a general continuous feature of objects extracted by the neural system. We consider the case that the range of possible values of the stimulus is much larger than the range of neuronal interactions. We can thus effectively take $x \in (-\infty, \infty)$ in our analysis. In simulations, however, we will set the stimulus range to be $-L/2 < x \leq L/2$, and impose a periodic condition accordingly.

Let $u(x, t)$ be the current at time $t$ in the neurons whose preferred stimulus is $x$. The dynamics of $u(x, t)$ is determined by the external input $I^{ext}(x, t)$, the network input from other neurons, and its own relaxation. It is given by

$$\tau_s \frac{\partial u(x, t)}{\partial t} = -u(x, t) + I^{ext}(x, t) + \rho \int_{-\infty}^{\infty} dx' J(x, x') p(x', t) \left[1 + f(x', t)\right] r(x', t), \quad [1]$$

where $\tau_s$ is the synaptic time constant, which is typically of the order 2 to 5 ms, and $\rho$ the neural density. $r(x, t)$ is the firing rate of neurons, which increases with the synaptic input, but saturates in the presence of global activity-dependent inhibition. A solvable model that captures these features is given by

$$r(x, t) = \frac{u(x, t)^2}{1 + k p \int_{-\infty}^{\infty} dx'' u(x'', t)^2}, \quad [2]$$

where $k$ is a positive constant controlling the strength of global inhibition. This type of global inhibition can be achieved by shunting inhibition [36, 37].

$J(x, x')$ is the baseline neural interaction from $x'$ to $x$ when no STP exists. In our solvable model, we choose $J(x, x')$ to be of the Gaussian form with an interaction range $\alpha$, i.e.,

$$J(x, x') = \frac{J_0}{\sqrt{2\pi}} \exp\left[-(x-x')^2/(2\alpha^2)\right], \quad [3]$$

where $J_0$ is a constant. $J(x, x')$ is translationally invariant, in the sense that it is a function of $x-x'$ rather than $x$ or $x'$. This is the key for generating the neutral stability of CANNs. The variable $p(x, t)$ represents the pre-synaptic STD effect, which has the maximum value of 1 and decreases with the firing rate of the neurons [20, 35]. Its dynamics is given by

$$\tau_a \frac{\partial p(x, t)}{\partial t} = 1 - p(x, t) - \tau_a \beta p(x, t) [1 + f(x, t)] r(x, t), \quad [4]$$

where $\tau_a$ is the time constant for synaptic depression, and the parameter $\beta$ controls the depression effect due to neural firing. The variable $f(x, t)$ represents the pre-synaptic STF effect, which increases with the firing rate of the neurons but saturates at a maximum value $f_{\text{max}}$. Its dynamics is given by

$$\tau_f \frac{\partial f(x, t)}{\partial t} = -f(x, t) + \tau_f \alpha [f_{\text{max}} - f(x, t)] r(x, t), \quad [5]$$

where $\tau_f$ is the time constant for synaptic facilitation, and the parameter $\alpha$ controls the facilitation effect due to neural firing.

The dynamical equations (3) and (4) are consistent with the phenomenological models of STD and STF fitted by experimental data [20] (see Supplement A). From Eqs. (1) and (5), we can calculate the steady state values of $p$ and $f$, which are

$$p = \frac{1}{1 + \tau_a \beta (1 + f)}, \quad [6]$$

$$f = \frac{f_{\text{max}} \tau_f \alpha}{1 + \tau_f \alpha}, \quad [7]$$
Hence, in the high frequency limit, \( \tau \alpha \sigma \gg 1 \), we have \( f \approx f_{\text{max}} \), which can be regarded as a constant, and \( p = 1/\left[1 + \tau_d \beta (1 + f_{\text{max}}) r \right] \). In this case, we only have to consider the effect of STD. On the other hand, in the low frequency limit, \( \tau_d \beta (1 + f_{\text{max}}) r \ll 1 \), we have \( p \approx 1 \) and only need to consider the effect of STF.

The Methods

Our theoretical analysis of the network dynamics is based on the observations that: 1) the stationary states of the network, as well as the profile of STP across all neurons, can be well approximated as Gaussian-shaped bumps; and 2) the state change of the network, and hence the profile of STP, can be well described by distortions of the Gaussian bump in various forms. We therefore can use a perturbation approach developed in [31] to solve the network dynamics analytically.

It is instructive for us to first review the network dynamics when no STP is included. This is done by setting \( \beta = 0 \) in Eq. (13) and \( \alpha = 0 \) in Eq. (14), so that \( p(x, t) = 1 \) and \( f(x, t) = 0 \) for all \( t \). In this case, the network can support a continuous family of stationary states when the global inhibition is not too strong (see Fig. 1). These steady states are

\[
\begin{align*}
\tilde{u}(x|z) &= u_0 \exp \left[ -\frac{(x-z)^2}{4a^2} \right], \\
\tilde{r}(x|z) &= r_0 \exp \left[ -\frac{(x-z)^2}{2a^2} \right],
\end{align*}
\]

where \( u_0 = |1 + (1 - k/k_c)^{1/2}] J_0/(4ak\sqrt{\pi}) \), \( r_0 = |1 + (1 - k/k_c)^{1/2}] / (2akp\sqrt{2\pi}) \) and \( k_c = \rho J_0^2/(8a\sqrt{2\pi}) \). These stationary states are translationally invariant among themselves and have the Gaussian shape with a free parameter \( z \) representing the peak position of the Gaussian bumps. They exist for \( 0 < k < k_c \), and \( k_c \) is the critical inhibition strength above which only silent states with \( u_0 = 0 \) exist.

Because of the translational invariance of the neuronal interactions, the dynamics of CANNs exhibits unique features. In [31] Fung et al. have shown that the wave functions of the quantum harmonic oscillators can well describe the different distortion modes of a bump state. For instance, during the process of tracking an external stimulus, the synaptic input \( u(x, t) \) can be written as

\[
u_n(x|z(t)) = \sum_{n=0}^{\infty} a_n(t) v_n(x|z(t)),
\]

where \( v_n(x|z(t)) \) are the wavefunctions of the quantum harmonic oscillator (Fig. 2).

\[
v_n(x|z) = (-1)^n (\sqrt{2a})^{n-1/2} \frac{\exp \left[ -(x-z)^2 \right]}{\sqrt{\pi} / 2a^n} \frac{d^n}{dx^n} \exp \left[ -(x-z)^2 / 2a^2 \right], \quad n = 0, 1, \ldots
\]

These functions have clear physical meanings, corresponding to distortions in the height, position, width, skewness and

---

**Fig. 1.** The \( N \) steady state solutions of the network with \( N \) neurons arranged in a ring. Note that each state is peaked at a neuron and has a common shape. Parameters: \( N = 16, a/L = 0.5/(2\pi), k/k_c = 0.5, \rho J_0 = 1 \). In the limit of many neurons, the stationary states will have the Gaussian-shape and can translate among themselves continuously.

**Fig. 2.** (a) - (d) The first distortion modes of the bump state. (e) - (h) Their effects of producing distortions, respectively, in the height, position, width and skewness of the Gaussian bump. Solid and dashed lines represent distorted and undistorted bumps respectively.

**Fig. 3.** (a) The neural response profile tracks the change of position of the external stimulus from \( z_0 = 0 \) to \( 3 \) at \( t = 0 \). Parameters: \( a = 0.5, \tau = 0.95, \tau_f = 0.0085, \rho J_0 A = 7.979 \). (b) The profile of \( u(x, t) \) at \( t/\tau = 0, 1, 2, \ldots, 10 \) during the tracking process in (a).

**Fig. 4.** Phase diagram of the network states with STD. Symbols: numerical solutions. Dashed line: Eq. (24). Dotted line: Eq. (25). Solid line: Gaussian approximation using 11th order perturbation of the STD coefficient. Point P: the working point for Figs. 7 and 8. Parameters: \( \tau_d/\tau_a = 50, \alpha = 0.5/6, \) range of the network \( x \in [-\pi, \pi] \).
other higher order features of the Gaussian bump (see Fig. 4). We can use a perturbation approach to solve the network dynamics effectively, with each distortion mode characterized by an eigenvalue determining its rate of evolution in time. A key property of CANNs is that the translational mode has a zero eigenvalue, and all other distortion modes have negative eigenvalues for $k < k_c$. This implies that the Gaussian bumps are able to track changes in the position of the external stimuli by continuously shifting the position of the bumps, with other distortion modes affecting the tracking process only in the transients. An example of the tracking process is shown in Fig 3, where we consider an external stimulus with a Gaussian profile given by

$$I^{\text{ext}}(x, t) = A \exp \left[ -\frac{(x - z(t))^2}{4a^2} \right]. \quad \text{[12]}$$

The stimulus is initially centered at $z = 0$, pinning the center of a Gaussian neuronal response at the same position. At time $t = 0$, the stimulus shifts its center from $z = 0$ to $z = 1.5$ abruptly. The bump moves towards the new stimulus position, and catches up with the stimulus change after a time duration, which is referred to as the reaction time.

We can generalize the perturbation approach developed in [11] to study the dynamics of CANNs with dynamical synapses. Since CANNs with STD exhibit more interesting dynamical behaviors than with STF, we will only present the approach in the case of STD. Extension to the case of STF is straightforward.

Similar to the synaptic input $u(x, t)$, the profile of STD can be expanded in terms of the distortion modes,

$$p(x, t) = 1 - \sum_{n=0}^{\infty} b_n(t) u_n(x, z(t)), \quad \text{[13]}$$

where $u_n(x, z)$ has a width $1/\sqrt{\alpha}$ times that of $u_n(x, z)$, $w_n(x, z) \equiv (\beta u_n(x, z))^{-1}$. We set $w_n = 1$ for simplicity. In terms of the coefficients $a_n(t)$ and $b_n(t)$, we get the dynamical equations for the coefficients $a_n(t)$ and $b_n(t)$. Details are presented in Appendix B.

The peak position $z(t)$ of the bump is determined from the self-consistent condition,

$$z(t) = \frac{\int_{-\infty}^{\infty} dx u(x, t) x}{\int_{-\infty}^{\infty} dx u(x, t)} \quad \text{[15]}$$

Truncating the perturbation expansion at increasingly high orders corresponds to the inclusion of increasingly complex distortions, and hence provides increasingly accurate descriptions of the network dynamics. As confirmed in the subsequent sections, the perturbative approach has an excellent agreement with simulation results. The agreement is especially remarkable when the STD strength is weak, and the lowest few orders are already sufficient to explain the dynamical features. The agreement is less satisfactory when STD is strong, and the perturbative approach typically overestimates the stability of the moving bump. This is probably due to the considerable distortion of the Gaussian profile of the synaptic depression when STD is strong.

### Phase Diagrams of CANNs with STP

We first study the impact of STP on the stationary states of CANNs when no external input is applied. For the convenience of analysis, we will explore the effects of STD and STF separately. This corresponds to the limits of high or low

neural firing frequencies, or the cases that only one type of STP dynamics is significant.

**The phase diagram of CANNs with STD.** We set $\alpha = 0$ in Eq. (5) to turn off STF. In the presence of STD, CANNs exhibit new interesting dynamical behaviors. Apart from the static bump state, the network also supports spontaneously moving bump states. Examining the steady state solutions of Eqs. (1) and (2) we find that $u_0$ scales as $\rho_0 \alpha_0^2$, and $1 - p(x, t)$ scales as $\tau_0 \beta_0^2$. Hence we introduce the dimensionless parameters $\tau \equiv k/k_c$ and $\beta \equiv \beta_0/(\rho_0^2 a_0^2)$. The phase diagram obtained by numerical solutions to the network dynamics is shown in Fig 1.

We first note that the synaptic depression and the global inhibition plays the same role in reducing the amplitude of the bump states. This can be seen from the steady state solution of $u(x, t)$, which reads

$$u(x) = \int_{-L}^{L} dx' \frac{\rho J(x - x') u(x')^2}{1 + k p \int dx'' u(x'')^2 + \tau \beta u(x')^2}. \quad \text{[16]}$$

The third term in the denominator of the integral arises from STD, and plays the role of a local inhibition that is strongest where the neurons are most active. Hence we see that the silent state with $u(x, t) = 0$ is the only stable state when either $\tau$ or $\beta$ is large.

When STD is weak, the network behaves similarly with CANNs without STD, that is, the static bump state is present up to $\mathcal{L}$ near 1. However, when $\beta$ increases, a state with the bump spontaneously moving at a constant velocity comes into existence. Such moving states have been predicted in CANNs [27, 28], and may be associated with travelling wave behaviors widely observed in the neocortex [29]. At an intermediate range of $\beta$, both the static and moving states coexist, and the final state of the network depends on the initial condition. When $\beta$ increases further, static bumps disappear. In the limit of high $\beta$, only the silent state is present. Below, we will use the perturbation approach to analyze the network dynamical behaviors.

**Zeroth Order: The Static Bump**

The zeroth order perturbation is applicable to the solution of the static bump, since the profile of the bump remains effectively Gaussian in the presence of synaptic depression. Hence, when STD is weak and for $a \ll L$, we propose the following Gaussian approximations,

$$u(x, t) = u_0(t) \exp \left[ -\frac{(x - z(t))^2}{4a^2} \right]. \quad \text{[17]}$$

$$p(x, t) = 1 - p_0(t) \exp \left[ -\frac{(x - z(t))^2}{2a^2} \right]. \quad \text{[18]}$$

As derived in Supplement C, the dynamical equations for $u_0$ and $p_0$ are given by

$$\tau_s \frac{du_0}{dt} = \frac{\beta u_0(t)^2}{4(1 + \beta u_0(t)^2)^2/8} \left[ 1 - \sqrt{\frac{4}{\beta u_0(t)}} - \beta u_0(t) + \beta \right], \quad \text{[19]}$$

$$\tau_s \frac{dp_0}{dt} = \frac{\beta u_0(t)^2}{1 + \beta u_0(t)^2)^2/8} \left[ 1 - \sqrt{\frac{2}{3 p_0(t)}} - p_0(t) \right]. \quad \text{[20]}$$
where $\tau \equiv p_J a_0$ is the dimensionless bump height and $\overline{A} \equiv p_J a A$ is the dimensionless stimulus strength. For $\overline{A} = 0$, the steady state solution of $\overline{\tau}$ and $p_0$ and its stability against fluctuations of $\overline{\tau}$ and $p_0$ are described in Supplement C. We find that stable solutions exist when

$$\beta \leq \frac{p_0(1 - \sqrt{4/\sqrt{\beta} p_0})^2}{4(1 - 2/\sqrt{\beta} p_0)} \left[1 + \frac{\tau_s}{\tau_d(1 - \sqrt{2/\sqrt{\beta} p_0})}\right], \quad [21]$$

when $p_0$ is the steady state solution of Eqs. (19) and (20). The boundary of this region is shown as a dashed line in Fig. 4. Unfortunately, this line is not easily observed in numerical solutions since the static bump is unstable against fluctuations that are asymmetric with respect to its central position. Although the bump is stable against symmetric fluctuations, asymmetric fluctuations can displace its position and eventually convert it to a moving bump. This will be considered in the first order perturbation in the next subsection.

**First Order: The Moving Bump**

When the network bump is moving, the profile of STD is lagging behind due to its slow dynamics, and this induces an asymmetric distortion in the profile of STD. Fig. 4 illustrates this behavior. Comparing the static and moving bumps shown in Fig. 4(a) and (b), one can see that the profile of a moving bump is characterized by a lag of the synaptic depression behind the moving bump. This is because neurons tend to be less active in the locations of low values of $p(x,t)$, causing the bump to move away from locations of strong synaptic depression. In turn, the region of synaptic depression tends to follow the bump. However, if the time scale of synaptic depression is large, the recovery of the synaptic depressed region is slowed down, and cannot catch up with the bump motion. Thus, the bump starts moving spontaneously. This is also the cause attributed to anticipative non-local events modeled in the hippocampus [34, 35].

To incorporate this asymmetry into the network dynamics, we consider the first order perturbation. However, to facilitate our analysis, we make a further simplification as follows:

$$u(x,t) = u_0(t) \exp \left(-\frac{(x-vt)^2}{4a^2}\right), \quad [22]$$

$$p(x,t) = 1 - p_0(t) \exp \left(-\frac{(x-vt)^2}{2a^2}\right) + p_1(t) \exp \left(-\frac{(x-vt)^2}{2a^2}\right) \left(\frac{x-vt}{a}\right). \quad [23]$$

This means that we have restricted the bump profile to the zeroth order. Comparison with the full first order perturbation shows that the discrepancy is not significant. This is because the synaptic interactions among the neurons effectively maintain the bump profile in a Gaussian shape, whereas the STD profile is much more susceptible to asymmetric perturbations. As described in Supplement D, we obtain four steady-state equations for $\overline{\tau}/B$, $p_0$, $p_1$, and $\tau_s/a$ in terms of the parameters $\beta \overline{\tau}^2/B$ and $\tau_s/\tau_d$, where $B \equiv 1 + \overline{\tau}^2/8$ is the global inhibition factor. It is easy to first check that the static bump obtained in Supplement C is also a valid solution when we set $v$ and $p_1$ to 0. We can then study the stability of the static bump against asymmetric fluctuations. This is done by introducing small values of $p_0$ and $\tau_s/a$ into the static bump solution and considering how they evolve. As shown in Supplement D, the static bump becomes unstable when

$$\frac{\overline{\tau}^2}{1 + \overline{\tau}^2/8} \leq Q \left[\frac{\tau_d}{\tau_s} - R + \sqrt{\left(\frac{\tau_d}{\tau_s} - R\right)^2 - S}\right]^{-1}, \quad [24]$$

where $Q = 7\sqrt{7}/4$, $R = (7/4)(5/2)\sqrt{7}/6 - 1$, and $S = (343/36)(1 - \sqrt{6/7})$. This means that in the region bounded by Eqs. (21) and (22), the static bump is unstable to asymmetric fluctuations. It is stable (or more precisely, metastable) when it is static, but once it is pushed to one side, it will continue to move along that direction. We call this behavior metastatic. As we shall see, this metastatic behavior is the cause of the enhanced tracking performance.

Next, we consider solutions with non-vanishing $p_1$ and $v$. We find that real solutions exist only if condition (24) is satisfied. This means that as soon as the static bump becomes unstable, the moving bump comes into existence. As shown in Fig. 4 the boundary of this region effectively coincides with the numerical solution of the line separating the static and moving phases. In the entire region bounded by Eqs. (21) and (22), the moving and the (meta)static bumps coexist.
We also find that when $\tau_d/\tau_s$ increases, the moving phase expands at the expense of the (pure) static phase. This is because the recovery of the synaptic depressed region becomes increasingly slow, making it harder to catch up with the changes in the bump motion, hence sustaining the moving bump.

The phase diagram of CANNs with STF. We set $\beta = 0$ in Eq. (4) to turn off STD. Comparing with STD, STF has qualitatively the opposite effect on the network dynamics. When an external perturbation is applied, the dynamical synapses will not push the neural bump away, but instead will try to pull the bump back to its original position. The phase diagram in the space of $\kappa$ and the rescaled STF parameter $v = \tau_s \alpha/(\rho^2 J_0^2)$ is shown in Fig. 8. When $\alpha$ increases, the range of inhibitory strength $\kappa$ allowing for a bump state is enlarged. Note that since STF tends to stabilize the bump states against asymmetric fluctuations, no moving bumps exist. The phase boundary of the static bump is well predicted by the second order perturbation.

Concerning the time scale of neural information processing, it should be noted that it takes time of the order $\tau_I$ for neuronal interactions to be fully facilitated. In the parameter range of $\kappa > 1$ where the facilitated neuronal interaction is necessary for holding a bump state, we need to present an external input for a time up to the order of $\tau_I$ before a bump state can be sustained.

Slow-Decaying States of CANNs with STD

The network dynamics displays a very interesting behavior in the marginally unstable region of the static bump. In this regime, the static bump solution just loses its stability. The bump is stable if the synaptic depression is fixed at a low level, but unstable at high level. Since the synaptic time scale is much shorter than that of STD, a bump can build up before the synaptic depression becomes effective. This maintains the bump in the plateau state with a slowly decaying amplitude, as shown in Fig. 7(a). After a time duration of the order $\tau_s$, the STD strength reaches a threshold, as shown in Fig. 7(b), and the bump state eventually decays to the silent state.

First Order: Trajectory Analysis. It is instructive to analyze the network behavior first by using the first order perturbation. We select a point in the marginally unstable regime of the silent phase, that is, in the vicinity of the static phase. As shown in Fig. 8, the nullclines of $\alpha$ and $p_0$ ($d\alpha/dt = 0$ and $dp_0/dt = 0$ respectively) do not have any intersections as they do in the static phase where the bump state exists. Yet, they are still close enough to create a region with very slow dynamics near the apex of the $\alpha$-nullcline at $\alpha/\beta = (8\kappa)^{1/2}, \sqrt{7}/4(1 - \sqrt{\kappa})$. Then, in Fig. 8 we plot the trajectories of the dynamics starting from different initial conditions.

The most interesting family of trajectories is represented by B and C in Fig. 8. Due to the much faster dynamics of $\alpha$, trajectories starting from a wide range of initial conditions converge rapidly, in a time of the order $\tau_s$, to a common trajectory in the close neighborhood of the $\alpha$-nullcline. Along this common trajectory, $\alpha$ is effectively the steady state solution of Eq. (19) at the instantaneous value of $p_0(t)$, which evolves with the much longer time scale of $\tau_d$. This gives rise to the plateau region of $\alpha$ which can survive for a duration of the order $\tau_d$. The plateau ends after the trajectory has passed the slow region near the apex of the $\alpha$-nullcline. This dynamics is in clear contrast with trajectory D, in which the bump height decays to zero in a time of the order $\tau_s$.

Trajectory A represents another family of trajectories having rather similar behaviors, although the lifetimes of their plateaus are not so long. These trajectories start from more depleted initial conditions, and hence do not have chances to get close to the $\alpha$-nullcline. Nevertheless, they converge rapidly, in a time of order $\tau_s$, to the band $\alpha \approx (8\kappa)^{1/2}$, where the dynamics of $\alpha$ is slow. The trajectories then rely mainly on the dynamics of $p_0$ to carry them out of this slow region, and hence plateaus of lifetimes of the order $\tau_d$ are created.

Following similar arguments, the plateau behavior also exists in the stable region of the static states. This happens when the initial condition of the network lies outside the basin of attraction of the static states, but it is still in the vicinity of the basin boundary.

When one goes deeper into the silent phase, the region of slow dynamics between the $\alpha$- and $p_0$-nullclines broadens. Hence plateau lifetimes are longest near the phase boundary between the bump and silent states, and become shorter when one goes deeper into the silent phase. This is confirmed by the contours of plateau lifetimes in the phase diagram shown in Fig. 9 obtained numerically. The initial condition is uniformly set by introducing an external stimulus $f(x,z_0) = \lambda (x^2/(4\alpha^2))$ to the right hand side of Eq. (21), where $\lambda$ is the stimulus strength. After the network has reached a steady state, the stimulus is removed at $t = 0$, leaving the network to relax. It is observed that the plateau behavior can be found in an extensive region of the parameter space.

Second Order: Lifetime Analysis. As shown in Fig. 7, the first order perturbation over-estimates the stability of the plateau
state, yielding lifetimes longer than the simulation results. The main reason is that the width of the synaptic depression profile is restricted to be a constant in the first order perturbation. However, the synaptic depression profile is broader than the bump. This can be seen from Eq. (1), recast in the form
\[
\tau_d \frac{\partial p(x,t)}{\partial t} = h(x,t) \left[ 1 - p(x,t) - \frac{\tau_d \beta r(x,t)}{1 + \tau_d \beta r(x,t)} \right], \quad [25]
\]
where \(h(x,t)\) is a function of \(x\) and \(t\). This shows that the neurotransmitter loss, \(1 - p(x,t)\), relaxes towards the Gaussian \(r(x,t)\), which is in turn normalized by the factor \(1 + \tau_d \beta r(x,t)\). This normalization factor is smaller where the firing rate is low, so that the profile of \(1 - p(x,t)\) is broader than the firing rate profile \(r(x,t)\).

To incorporate the effects of broadened STD profile, we introduce the second order perturbation. Dynamical equations are obtained by truncating the equations in Appendix beyond the second order. As shown in Fig 7, the second order perturbation yields a much more satisfactory agreement with simulation results when compared with lower order perturbations.

Decoding Performances of CANNs with STF
CANNs have been interpreted as an efficient framework for neural systems implementing population decoding [19]. Consider the reading-out of an external feature \(z_0\) from noisy inputs by CANNs. For example, \(z_0\) may represent the moving direction of an object. In the decoding paradigm, a CANN responds to an external input \(I^{ext}(x)\) with a bump state \(r(x|z)\), where the peak position of the bump \(\tilde{z}\) is interpreted as the decoding result of the network.

In the presence of STF, neuronal connections are facilitated around the area where neurons are most active. With this additional feature, the network decoding will be determined not only by the instantaneous input, but also by the recent history of external inputs. Consequently, temporal fluctuations in external inputs are largely averaged out, leading to improved decoding accuracies.

We consider an external input given by
\[
I^{ext}(x,t) = A \exp \left[ - \frac{(x - z_0 - \eta(t))^2}{4a^2} \right], \quad [26]
\]
where \(z_0\) represents the true stimulus value, and \(\eta(t)\) white noise of zero mean and satisfies \((\eta(t)\eta(t')) = 2T a^2 \delta(t - t')\) with \(T\) denoting the noise strength.

In the presence of weak noise, the position of the bump state is found to be centered at \(z_0 + \sigma(t)\), as derived in Supplement E. Hence, the decoding error of the network is measured by the variance of the bump position over time, namely, \((\sigma(t)^2)\). Fig 10 shows the typical decoding performance of the network with STFs

**Fig. 10.** (color online) The typical decoding performances of the network with and without STF. Parameter: \(N = 80, \alpha = 0.5, x \in [-\pi, \pi]\) \(\beta = 0.25, \Gamma = 1.596\) and \(T = 0.02\).

**Fig. 11.** The decoding errors of the network vs. different levels of noise. Parameters other than \(T\) are the same as in Fig 10.

**Fig. 12.** The response of CANNs with STD to an abruptly changed stimulus from \(z_0/a = 0\) to \(z_0/a = 3.0\) at \(t = 0\). Symbols: numerical solutions. Lines: Gaussian approximation using 11th order perturbation of the STD coefficient. Parameters: \(\tau_d/\tau_s = 50, \Lambda = 7.9788, N = 80, a = 0.5\) and \(x \in [-\pi, \pi]\).

**Fig. 13.** Tracking of a neuronal bump with continuously moving stimulus. Symbols: simulation result of the peak of the bump. Dashed line: 11th order perturbation prediction. Solid line: Continuously moving stimulus with speed \(\tau_d/\tau_s = 0.06\). Parameters: \(\overline{\sigma} = 1.5958, \overline{\beta} = 0.5\). (A) \(\overline{\sigma} = 0.01\). (B) \(\overline{\sigma} = 0.05\). Other parameters are the same as Fig 12.

**Fig. 14.** Comparison of tracking performance between CANN with constant couplings, CANN with synaptic depression and CANN with facilitation. Parameters: \(\overline{\sigma} = 7.9788, \tau_d/\tau_s = 50\) and \(\tau_f/\tau_s = 50\).
network with or without STF. We see that with STF, the fluctuation of the bump position is reduced significantly. Fixing the bump shifts to the new position faster. When compared with the case without STD, we find that Fig. 12 shows the network responses during the tracking process. How long it takes for the network to catch up this change.

Tracking Performance of CANNs with STP

A key property of CANNs is their capacity of tracking time-varying stimuli, which lays the foundation for CANNs to implement spatial navigation, population decoding, and update of head-direction memory. We investigate how STP affects the tracking performance of CANNs. In general, there is a trade-off between the stability of network states and the capacity of the network tracking time-varying stimuli. Since STD and STF have opposite effects on the mobility of the network states, we expect that they will also have opposite impact on the tracking performance of CANNs.

We first investigate the impact of STD. An external stimulus \( R_0^{\text{ext}}(x) = A \exp(-|x - z_0|^2/(4\sigma^2)) \) is applied to the right hand side of Eq. (22), with \( z_0 \) the position of the stimulus. We consider a tracking task in which the stimulus value \( z_0 \) abruptly changes at \( t = 0 \) to a new value, and measure how long it takes for the network to catch up this change. Fig. 12 shows the network responses during the tracking process.

Compared with the case without STD, we find that the bump shifts to the new position faster. When \( \beta \) is too strong, the bump may overshoot the target before eventually approaching it. As remarked previously, this is due to the metastatic behavior of the bumps, which enhances their reaction to move from the static state when a small push is exerted.

We also study the tracking of an external stimulus moving with a constant velocity \( v \). As shown in Fig. 13(a), for the case of weak of STD, the initial speed of the bump is almost zero. Then, when the stimulus is moving away, the bump accelerates in an attempt to catch up with the stimulus. After some time, the separation between the bump and the stimulus converges to a constant. This tracking behavior is similar to the case without STD. The tracking behavior in the case of strong STD is more interesting. As shown in Fig. 13(b), the bump position eventually overtakes the stimulus, displaying an anticipative behavior. This can be attributed to the metastatic property of STD.

We further explore how STF affects the tracking performance of CANNs. As expected, STF degrades the tracking performance of CANNs (see Fig. 14). The larger the STF strength, the slower the tracking speed of the network.

Discussions

In the present study, we have investigated the impact of STD and STF on the dynamics of CANNs and their potential roles in neural information processing. We have analyzed the dynamics using successive orders of perturbation. The perturbation analysis works well when STD is not too strong, although it over-estimates the stability of the bumps when STD is strong. The zeroth order analysis accounts for the Gaussian shape of the bump, and hence can predict the boundary of the static phase satisfactorily. The first order analysis includes the displacement mode and asymmetry with respect to the bump peak, and hence can describe the onset of the moving phase. Furthermore, it provides insights on the metastatic nature of the bumps and its relation with the enhanced tracking performance. The second order analysis further includes the width distortions, and hence improves the prediction of the boundary of the moving phase, as well as the lifetimes of the plateau states. Higher order perturbations are required to yield more accurate descriptions of results such as the overshooting in the tracking process.

More important, our work reveals a number of interesting behaviors which may have far-reaching implications in neural computation.

First, with STD, CANNs can support both static and moving bumps. Static bumps exist only when the synaptic depression is sufficiently weak. A consequence of synaptic depression is that it places static bumps in the metastatic state, so that its response to changing stimuli is speeded up, enhancing its tracking performance. The moving bump states may be associated with the travelling wave behaviors widely observed in the hippocampus. Interestingly, for strong STD, the network state can even overtake the moving stimulus, reminiscent of the phase precessing behavior of place cells in the hippocampus [31].

Second, STD endows CANNs with slow-decaying behaviors. When a network is initially stimulated to an active state by an external input, it will decay to silence very slowly after the input is removed. The duration of the plateau is of the time scale of STD rather than neural signaling, and this provides a way for the network to hold the stimulus information for up to hundreds of milliseconds, if the network operates in the parameter regime that the bumps are marginally unstable. This property is, on the other hand, extremely difficult to be implemented in attractor networks without STD. In a CANN without STD, an active state of the network will either decay to silence exponentially fast or be retained forever, depending on the initial activity level of the network. Indeed, how to shut off the activity of a CANN has been a challenging issue that received wide attention in theoretical neuroscience, with solutions suggesting that a strong external input either in the form of inhibition or excitation must be applied (see, e.g., [32]). Here, we show that STD provides a mechanism for closing down network activities naturally and in the desirable duration. Taking into account the time scale of STD (of the order 100 ms) and the passive nature of its dynamics, the STD-based memory is most likely to be associated with the sensory memory of the brain, e.g., the iconic and the echoic memories [10].

Third, STF improves the decoding accuracy of CANNs. When an external stimulus is presented, STF strengthens the interactions among neurons which are tuned to the stimulus. This stimulus-specific facilitation provides a mechanism for the network to hold a memory trace of external inputs up to the time scale of STF, and this information can be used by the neural system for executing various memory-based operations, such as the working memory. We test this idea in a population decoding task, and find out that the error is indeed decreased. This is due to that the determination of the network response by both the instantaneous value and the history of external inputs, which effectively averages out temporal fluctuations.

These computational advantages of dynamical synapses lead to the following implications about the modeling of neural systems. First, it sheds some light on the long standing debate in the field about the instability of CANNs to noises. Two aspects of instability have been concerned [28, 11]. One is the structural instability, which refers to the argument that network components in reality, such as the neuronal synapses, are unlikely to be as perfect as mathematically required in CANNs. A small amount of discrepancy in the network structure can destroy the state space considerably, destabilizing the bump state after the stimulus is removed. The other instability refers to the computational sensitivity of the network to input noises. Because of neutral stability, the bump position is very susceptible to fluctuations in external inputs,
rendering the network decoding unreliable. We have shown that STF can largely improve the computational robustness of CANNs by averaging out the temporal fluctuations in inputs. Similarly, STF can overcome the structural susceptibility of CANNs. With STF, the neuronal connections around the bump area are strengthened temporally, which effectively stabilizes the bump in the time scale of STF. Another mechanism having a similar spirit is to reduce the inhibition strength around the bump area [12].

Second, we have investigated the impact of STD and STF on the tracking performance of CANNs. There is, in general, a trade-off between the stability of bump states and the tracking performance of the network. STD increases the mobility of bump states and hence the tracking speed of the network, whereas STF has the opposite effect. These differences predict that in cortical areas where time-varying stimuli, such as the head and the moving direction of objects, are encoded, we should observe that STD has a stronger effect than STF. On the other hand, in cortical areas where the robustness of bump states, i.e., the decoding accuracy of stimuli, is preferred, we should observe that STF has a stronger effect.

Third, we have shown that both STD and STF can generate short-term memories, but their ways of achieving it are quite different. In STD, the memory is held in the prolonged neural activities, whereas in STF, it is in the facilitated neuronal connections. Mongillo et al. [13] proposed that with STF, neurons may not even have to be active after the stimulus is removed. The facilitated neuronal connections, mediated by the elevated calcium residue, is sufficient to carry out the memory retrieval. In our model, this is equivalent to setting the network to be in the parameter regime without static bump solutions, or in the regime having static bump solutions but the external stimulus is not presented long enough to fully facilitate neuronal interactions. Thus, taking into account the energy consumption associated with neural firing, the STF-based mechanism for short-term memory has the advantage of being economically efficient. However, the STD-based one also has a desirable property of enabling the stimulus information to be propagated to other cortical areas, since neural firing is necessary for signal transmission, and this is critical in the early information pathways. Furthermore, the time durations required for eliciting STP- and STD-based memory are significantly different. For the former, it needs a stimulus to be presented up to \( \tau_2 \) amount of time for facilitating neuronal interactions sufficiently; whereas, for the latter, a transient appearance of a stimulus is adequate. This difference implies that the two memory mechanisms may have potentially different applications in neural systems.

In summary, we have revealed that STP can play very valuable roles in neural information processing, including achieving short-term memory, improving decoding accuracy, enhancing tracking performance and stabilizing CANNs. We have also shown that STD and STF tend to have different impact on the network dynamics. These results, together with the fact that STP displays large diversity in the neural cortex, suggest that the brain may employ a strategy of weighting STD and STF differentially for serving different computational tasks. In the present study, for the simplicity of analysis, we have only explored the effects of STD and STP separately. In practice, a proper combination of STD and STP can make the network exhibits new interesting behaviors and implements new computationally desirable properties. For instance, a CANN with both STD and STF, and with the time scale of the former shorter than that of the latter, can hold bump states for a period of time before shifting the memory to facilitated neuronal connections. This enables the network to achieve both goals of conveying the stimulus information to other cortical areas and holding the memory cheaply. Alternatively, the network may have the time scale of STD longer than that of STF, so that the network can have improved encoding results for external stimuli and is also able to close down bump activities easily. We will explore these interesting issues in the future.

Appendix: The Perturbation Approach for Solving the Dynamics of CANNs with STD

Substituting Eqs. (10) and (13) into Eq. (1), the right-hand sides becomes

\[
\frac{\rho}{B} \left[ \sum_{nm} a_n a_m \int dx' J(x, x') v_n(x', t) v_m(x', t) - \sum_{nm} b_n b_m \int dx' J(x, x') v_n(x', t) v_m(x', t) w_j(x', t) \right] - \sum_n a_n(t) v_n(x, t) + I^{ext}(x, t). \tag{27}
\]

This expression can be resolved into a linear combination of the distortion modes \( v_k(x, t) \). The coefficients of these modes are obtained by multiplying the expression with \( v_k(x, t) \) and integrating \( x \). Using the orthonormal property of the distortion modes, we have

\[
\sum_k w_k(x, t) \left[ \frac{\rho J_0}{B} \left( \sum_{nm} \mathcal{C}_{nm}^k a_n a_m - \sum_{nm} \mathcal{D}_{nm}^k a_n a_m b_l \right) - a_k + I_k \right], \tag{28}
\]

where

\[
\mathcal{C}_{nm}^k \equiv \int dx'' \int dx'' J(x'', x') v_k(x'', t) v_n(x', t) v_m(x', t), \tag{29}
\]

\[
\mathcal{D}_{nm}^k \equiv \int dx'' \int dx'' J(x'', x') v_k(x'', t) v_n(x', t) v_m(x', t) w_j(x', t), \tag{30}
\]

and \( I_k(t) \) is the \( k \)-th component of \( I^{ext}(x, t) \). Similarly, the right-hand side of Eq. (4) becomes

\[
- \sum_k w_k(x, t) \left[ -b_k + \frac{\tau_d J_0}{B} \left( \sum_{nm} \mathcal{C}_{nm}^k a_n a_m - \sum_{nm} \mathcal{D}_{nm}^k a_n a_m b_l \right) \right], \tag{31}
\]

where

\[
\mathcal{C}_{nm}^k \equiv \int dx'' w_k(x'', t) v_n(x', t) v_m(x', t), \tag{32}
\]

\[
\mathcal{D}_{nm}^k \equiv \int dx'' w_k(x'', t) v_n(x', t) v_m(x', t) w_j(x', t). \tag{33}
\]

We choose \( v_n(x, t) = v_n(x - z(t)) \) and \( w_n(x, t) = w_n(x - z(t)) \). Using the following relationship of Hermite polynomials

\[
H_{n+1}(x) = 2xH_n(x) - 2nH_{n-1}(x), \quad H'_n(x) = 2nH_{n-1}(x), \tag{34}
\]

we have \( \dot{v}_n = (\dot{z}/(2a))(\sqrt{n+1}v_{n-1} - \sqrt{n}v_n) + \dot{w}_n = (\dot{z}/(2a))(\sqrt{n}w_{n-1} - \sqrt{n+1}w_n) \). Making use of othornor-
mality of \( u_n \)'s and \( w_n \)'s, we have

\[
\tau_s \left[ \frac{\dot{a}_k}{\alpha} = -a_k + \frac{\rho_J}{B} \left( \sum_{nm} c_{nm} a_n a_m - \sum_{nm} b_{nm} a_n a_m b_{lm} \right) \right],
\]

\[
\tau_d \left[ \frac{\dot{b}_k}{\beta} = -b_k + \frac{\tau_d \beta}{B} \left( \sum_{nm} c_{nm} a_n a_m - \sum_{nm} b_{nm} a_n a_m b_{lm} \right) \right],
\]

where \( \tau_s \) and \( \tau_d \) are the STF and STD parameters, respectively, subject to \( \beta \geq \alpha \).

**B: The Recurrence Relations of the Perturbation Coefficients**

\[
\mathcal{C}_{nm}^k = \frac{1}{2} \left( \sqrt{n} c_{nm}^k + \sqrt{m} c_{nm}^k \right),
\]

\[
\mathcal{D}_{nm}^k = \frac{-1}{4} \sqrt{\frac{n}{m}} c_{nm}^k + \frac{3}{4} \sqrt{\frac{m}{n}} c_{nm}^k + \sqrt{\frac{1}{2}} \frac{\sqrt{n}}{\sqrt{m}} c_{nm}^k,
\]

\[
\mathcal{E}_{nm}^k = \frac{-1}{4} \sqrt{\frac{m}{n}} c_{nm}^k + \frac{3}{4} \sqrt{\frac{n}{m}} c_{nm}^k + \frac{1}{2} \frac{\sqrt{m}}{\sqrt{n}} c_{nm}^k,
\]

\[
\mathcal{D}_{nm}^{k+1} = \frac{6}{7} \left( \sqrt{\frac{1}{7}} \sqrt{\frac{m}{n}} c_{nm}^{k+1} + \sqrt{\frac{m}{n}} c_{nm}^{k+1} + \sqrt{\frac{1}{7}} \sqrt{\frac{n}{m}} c_{nm}^{k+1} \right) - \frac{1}{7} \sqrt{\frac{1}{7}} \sqrt{\frac{n}{m}} c_{nm}^{k+1}.
\]

\[
\mathcal{E}_{nm}^{k+1} = -\frac{1}{2} \sqrt{\frac{m}{n}} c_{nm}^{k+1} + \frac{1}{2} \sqrt{\frac{n}{m}} c_{nm}^{k+1} + \frac{1}{2} \frac{\sqrt{n}}{\sqrt{m}} c_{nm}^{k+1},
\]

**Supplemental Materials**

**A: Consistency with the Model of Tsodyks et al**

In the model of Tsodyks et al [20], STD is modeled by considering \( p \) to be the fraction of utilizable neurotransmitters, and STF is modeled by introducing \( U_0 \) to be the release probability of the neurotransmitters. The release probability \( U_0 \) relaxes to a nonzero constant, \( u_0 \), at some point after the arrival of a spike, and is enhanced at the arrival of a spike by an amount \( u_0(1-U_0) \). Hence the dynamics of \( p \) and \( U_0 \) are given by

\[
\tau_s \frac{\partial u_0}{\partial t} = I_{ext} - u_0 + \rho \int dx' J(x-x')p(x')U_1(x')r(x'),
\]

\[
\tau_d \frac{\partial p}{\partial t} = 1 - p - U_0 \tau_d p r,
\]

\[
\tau_d \frac{\partial U_0}{\partial t} = u_{ext} - U_0 + u_0(1-U_0) \tau_f r,
\]

where \( U_1 \equiv U_0 + u_0(1-U_0) \) is the release probability of the neurotransmitters after the arrival of a spike, and the \( x \) and \( t \) dependence of \( u_0 \), \( p \), and \( r \) are omitted in the above equations for convenience. Eliminating \( U_0 \), substituting \( \alpha \) and \( \beta \) via \( \alpha = u_0 \), \( \beta = u_0 + (1-u_0)u_{ext} \), \( U_1 = u_0(1-U_0)u_{ext} \), \( f_m = \{1+(1-U_0)u_{ext}\} \), and \( \tau_f = \{1+\beta\} \), we obtain equations [1], [2] and [3]. \( \alpha \) and \( \beta \) are the STF and STD parameters respectively, subject to \( \beta \geq \alpha \).
Without loss of generality, we let the equation simplifies to \( \tau \) derivatives in Eqs. (19) and (20) to zero, yielding

\[
\mathcal{J}_{nml} = -\frac{2}{3} \sqrt{\frac{m}{m}} \mathcal{J}_{nml} + \frac{1}{3} \sqrt{\frac{n}{m}} \mathcal{J}_{nml} \\
+ \sqrt{\frac{2}{3}} \left( \sqrt{\frac{m}{m}} \mathcal{J}_{nml} + \sqrt{\frac{k}{m}} \mathcal{J}_{nml} \right). \quad [S17]
\]

Since \( \mathcal{J}_{nml}^{0}, \mathcal{J}_{nml}^{00}, \mathcal{J}_{nml}^{0} \) and \( \mathcal{J}_{nml}^{000} \) can be calculated explicitly, all other \( \mathcal{J}_{nml}^{0}, \mathcal{J}_{nml}^{00}, \mathcal{J}_{nml}^{0} \), and \( \mathcal{J}_{nml}^{000} \) can be deduced.

### C: Static Bump: Lowest Order Perturbation

Without loss of generality, let \( \omega = 0 \). Substituting Eqs. (17) and (18) into Eq. (1), we get

\[
\tau_{a} e^{-\frac{2}{3} d_{a}} \frac{d v_{a}}{d t} = -\rho J_{0} u_{0} \frac{2}{\sqrt{2}} \left( 1 + \sqrt{2} \pi k \rho u_{0} \right) \left( e^{-\frac{2}{3} x_{a}^{2}} - \rho_{o} e^{-\frac{2}{3} x_{a}^{2}} \right) \quad - u_{0} e^{-\frac{2}{3} x_{a}^{2}} + A e^{-\frac{2}{3} x_{a}^{2}}. \quad [S18]
\]

Using the projection onto the \( v_{a} \), we can approximate \( \exp(-x_{a}^{2}/a^{2}) \approx \sqrt{\beta}/7 \exp(-x_{a}^{2}/4a^{2}) \). This reduces the equation to

\[
\tau_{a} e^{-\frac{2}{3} x_{a}^{2}} \frac{d u_{a}}{d t} = -u_{0} + \rho J_{0} u_{0} \frac{2}{\sqrt{2}} \left( 1 + \sqrt{2} \pi k \rho u_{0} \right) \left( 1 - \frac{\beta}{7} u_{0} \right) + A. \quad [S19]
\]

Introducing the rescaled variables \( \mathcal{V} \) and \( \mathcal{K} \), we get Eq. (19).

Similarly, substituting Eqs. (17) and (18) into Eq. (1), we get

\[
\tau_{a} e^{-\frac{2}{3} p_{a}} \frac{d p_{a}}{d t} = -p_{0} e^{-\frac{2}{3} x_{a}^{2}} + \frac{\tau_{d} \beta u_{0}^{2}}{1 + \sqrt{2} \pi k \rho u_{0} \left( e^{-\frac{2}{3} x_{a}^{2}} - \rho_{o} e^{-\frac{2}{3} x_{a}^{2}} \right)}. \quad [S20]
\]

Making use of the projection \( \exp(-x_{a}^{2}/a^{2}) \approx \sqrt{2}/3 \exp(-x_{a}^{2}/2a^{2}) \), the equation simplifies to

\[
\tau_{a} e^{-\frac{2}{3} p_{a}} \frac{d p_{a}}{d t} = -p_{0} + \frac{\tau_{d} \beta u_{0}^{2}}{1 + \sqrt{2} \pi k \rho u_{0} \left( 1 - \frac{\beta}{3} u_{0} \right)}. \quad [S21]
\]

Rescaling the variables \( u, k, \beta \) and \( A \), we get Eq. (20).

The steady state solution is obtained by setting the time derivatives in Eqs. (19) and (20) to zero, yielding

\[
\mathcal{V} = \frac{1}{\sqrt{2}} \frac{\beta}{B} \left( 1 - \frac{\beta}{7} p_{0} \right). \quad [S22]
\]

\[
\rho_{0} = \frac{\beta}{\sqrt{2} B} \left( 1 - \frac{\beta}{3} p_{0} \right). \quad [S23]
\]

where \( B \equiv 1 + \frac{k}{\rho} \sqrt{2} / 8 \) is the dissipation inhibition.

Dividing Eq. (S22) by (S23), we eliminate \( B \),

\[
\mathcal{V} = \frac{1}{\sqrt{2} \beta} \frac{\beta}{B} \left( 1 - \frac{\sqrt{2}}{1 - \frac{\sqrt{2}}{3} p_{0}} \right) \left( \frac{\beta}{7} p_{0} \right) \quad [S24]
\]

We can eliminate \( \mathcal{V} \) from Eq. (S25). This gives rise to an equation for \( p_{0} \)

\[
\frac{1}{2} p_{0} \left[ 1 - \frac{\sqrt{2}}{7} p_{0} \right]^{2} - \frac{1}{2} \left( \frac{\beta}{3} + \frac{k}{\rho} \right) p_{0} \left( 1 - \frac{\sqrt{2}}{3} p_{0} \right) - \left( 1 - \frac{\sqrt{2}}{3} p_{0} \right)^{2} = 0. \quad [S25]
\]

Rearranging the terms, we have

\[
\mathcal{T} = \frac{8}{p_{0}} \left( 1 - \frac{\beta}{3} p_{0} \right)^{2} - \frac{16}{p_{0}} \left( 1 - \frac{\sqrt{2}}{3} p_{0} \right)^{2} = 0. \quad [S26]
\]

Therefore, for each fixed \( p_{0} \), we can plot a parabolic curve in the space of \( \beta \) versus \( \kappa \). The dashed lines in Fig. S1(a) are parabolas for different values of \( p_{0} \). The family of all parabolas map out the region of existence of static bumps.

### Stability of the Static Bump

To analyze the stability of the static bump, we consider the time evolution of \( \epsilon = \mathcal{T}(t) - \mathcal{T} \) and \( \delta = p_{0}(t) - p_{0} \), where \( (\mathcal{T}, p_{0}) \) is the fixed point solution of Eqs. (S22) and (S23). Then, we have

\[
\frac{d}{dt} \begin{pmatrix} \epsilon \\ \delta \end{pmatrix} = \begin{pmatrix} A_{\kappa} & A_{\delta} \\ A_{\kappa} & A_{\delta} \end{pmatrix} \begin{pmatrix} \epsilon \\ \delta \end{pmatrix}. \quad [S27]
\]

where \( A_{\kappa} = -1/\tau_{a} + \sqrt{2}/(1 - \frac{\sqrt{2}}{3} p_{0} / \tau_{a} B^{2} \right), A_{\delta} = -\mathcal{T}/(1 - \frac{\sqrt{2}}{3} p_{0} / \tau_{a} B^{2} \right), A_{\kappa} = 2 \mathcal{T}/(1 - \frac{\sqrt{2}}{3} p_{0} / \tau_{a} B^{2} \right), A_{\delta} = -1/\tau_{a} - \sqrt{2}/(1 - \frac{\sqrt{2}}{3} p_{0} / \tau_{a} B^{2} \right). \) The stability condition is determined by the eigenvalues of the stability matrix, \( (T + 1 - \frac{\sqrt{2}}{3} p_{0} / \tau_{a} B^{2} \right) / 2 \), where \( D \) and \( T \) are the determinant and the trace of the matrix respectively. Using Eqs. (S22) and (S27), the determinant and the trace can be simplified to

\[
D = \frac{1}{\tau_{a} \tau_{d} B} \left( \frac{2 \sqrt{2}}{T_{a} B} - \frac{2}{1 - \frac{\sqrt{2}}{3} p_{0}} \right), \quad [S28]
\]

\[
T = \frac{2}{B} - \frac{\tau_{a}}{\tau_{d} \left( 1 - \frac{\sqrt{2}}{3} p_{0} \right)} - 1. \quad [S29]
\]

The static bump is stable if the real parts of the eigenvalues are negative. The eigenvalues are real when \( T^{2} \geq 4D \). This corresponds to a non-oscillating solutions. After some algebra, we obtain the boundary \( T^{2} = 4D \) given by

\[
\beta = \frac{p_{0} \left( 1 - \frac{\sqrt{2}}{3} p_{0} \right)^{2} + \tau_{a} p_{0} \left( 1 - \frac{\sqrt{2}}{3} p_{0} \right)^{2}}{4 \left( 1 - \frac{\sqrt{2}}{3} p_{0} \right)} \quad [S30]
\]

This boundary is shown in Fig. S1(b). Below this boundary, the stability condition can be obtained as

\[
\beta \leq \frac{p_{0} \left( 1 - \frac{\sqrt{2}}{3} p_{0} \right)^{3}}{4 \left( 1 - \frac{\sqrt{2}}{3} p_{0} \right) \left( 1 - \frac{\sqrt{2}}{3} p_{0} + \sqrt{8/21} p_{0}^{2} \right)} \quad [S31]
\]

This upper bound is identical to the existence condition of (S20), which is above the boundary of non-oscillating solutions. This implies that all non-oscillating solutions are stable.

Above the boundary (S20), the convergence to the steady state becomes oscillating, and the stability condition reduces to \( T \leq 0 \), yielding Eq. (21). This condition narrows the region of static bump considerably, as shown in Fig. S1(b).
D: Moving Bump: Lowest Order Perturbation

We substitute Eqs. (22) into Eqs. (1) and (4). Eq. (1) becomes an equation containing \( \exp[-(x-vt)^2/4a^2] \) and \( \exp[-(x-vt)^2/4a^2]/a \), after we have made use of the projections \( \exp[-(x-vt)^2/3a^2] \approx \sqrt{b/a} \exp[-(x-vt)^2/4a^2] \), and \( \exp[-(x-vt)^2/3a^2]/(x-vt)/a \approx (\sqrt{b/a})^3 \exp[-(x-vt)^2/4a^2]/(x-vt)/a \).

Equating the coefficients of \( \exp[-(x-vt)^2/4a^2] \) and \( \exp[-(x-vt)^2/4a^2]/a \), and rescaling the variables, we arrive at

\[
\tau_a \frac{d}{dt} p_1 = p_0 - \beta a^2 \left( 1 - \sqrt{\frac{2}{3}} p_0 \right), \quad \tau_a \frac{d}{dt} p_0 = \left[ 1 + \beta a^2 \left( \frac{2}{3} \right) \right] p_1. \tag{S32}
\]

Similarly, making use of the projections \( \exp[-(x-vt)^2/2a^2] \approx \sqrt{2/3} \exp[-(x-vt)^2/2a^2] \), \( \exp[-(x-vt)^2/2a^2](x-vt)/a \approx (\sqrt{2/3})^3 \exp[-(x-vt)^2/2a^2](x-vt)/a \), we find that Eq. (4) gives rise to

\[
\tau_s \frac{d}{dt} p_1 = p_0 - \beta a^2 \left( 1 - \sqrt{\frac{2}{3}} p_0 \right), \quad \tau_s \frac{d}{dt} p_0 = \left[ 1 + \beta a^2 \left( \frac{2}{3} \right) \right] p_1. \tag{S33}
\]

The solution can be parametrized by \( \xi \equiv \beta \tau / B \),

\[
p_0 = \frac{2}{\sqrt{3}} \left[ 1 + \left( \frac{4}{3} \right)^{3/2} \xi \right] G(\xi), \quad \frac{\tau_a}{B} = \sqrt{\frac{2}{3}} \left( \frac{2}{3} \right)^{3/2} \frac{\tau_a}{B} G(\xi),
\]

\[
\frac{\tau_s}{a} = \frac{\sqrt{2} \tau}{\tau_s} F(\xi), \quad p_1 = \frac{\sqrt{2} \tau}{\tau_s} F(\xi). \tag{S35}
\]

where \( F(\xi) = (4/7)^{3/2} \xi - (\tau_s / \tau_a) [1 + (2/3)^{3/2} \xi] [1 - (\sqrt{2/3} - \sqrt{4/7}) \xi] \), and \( G(\xi) = (4/7)^{1/2} + (4/7)^{1/2} (\tau_s / \tau_a) [1 + (2/3)^{3/2} \xi] \). Real solution exists only if Eq. [23] is satisfied. The solution enables us to plot the contours of constant \( \xi \) in the space of \( \tau / B \) and \( \tau / B \). Using the definition of \( \xi \), we can write

\[
\kappa = \frac{8}{\xi^2} - \frac{8}{\xi^2} \left( \frac{\tau_a}{B} \right)^2 c^2, \tag{S36}
\]

where the quadratic coefficient can be obtained from Eq. (S35). Fig. 2(a) shows the family of curves with constant \( \xi \) each with constant bump velocity. The lowest curve saturates the inequality in Eq. (13), and yields the boundary between the static and metastatic or moving regions in Fig. 2(a). Considering the stability condition in the next subsection, only the stable branches of the parabolas are shown.

**Stability of the Moving Bump** To study the stability of the moving bump, we consider fluctuations around the moving bump solution. Suppose

\[
u(x,t) = (u_0 + u_1) e^{-(x-vt-s)^2/4a^2}, \tag{S37}
\]

\[
p(x,t) = 1 - (p_0 + p_1) e^{-(x-vt-s)^2/2a^2} + (p_1 + \epsilon_1) \left( x - vt + s \right) e^{-(x-vt-s)^2/2a^2}, \tag{S38}
\]

These expressions are substituted into the dynamical equations. The result is

\[
\tau_a \frac{d}{dt} \bar{u}_1 = \sqrt{\frac{2\pi}{B^2}} \left( 1 - \sqrt{\frac{4}{7}} \alpha_0 \right) \bar{u}_1 - \sqrt{\frac{2}{7}} \alpha_0 - \bar{u}_1, \tag{S39}
\]

\[
\tau_s \frac{d}{dt} \bar{u}_1 + \frac{4 \alpha_1}{B^2} \left( \frac{2}{7} \right)^{3/2} \bar{u}_1 + \frac{2 \alpha_1}{B} \left( \frac{2}{7} \right)^{3/2} \epsilon_1, \tag{S40}
\]

\[
\tau_d \frac{d}{dt} \bar{u}_0 = \frac{4 \pi \bar{u}_1}{B^2} \left( 1 - \sqrt{\frac{2}{7}} \alpha_0 \right) \bar{u}_1 - \left( 1 + \sqrt{\frac{2}{7}} \xi \right) \epsilon_0 \tag{S41}
\]

\[
\tau_d \frac{d}{dt} \bar{u}_1 + \frac{\sqrt{2} \tau_s}{2 \alpha_1} \epsilon_1 - \frac{\tau_s p_1}{2 \alpha_1} \frac{d}{dt} \bar{u}_1 \tag{S42}
\]

We first revisit the stability of the static bump. By setting \( \nu \) and \( p_1 \) to 0, considering the asymmetric fluctuations \( s \) and \( \epsilon_1 \).
in Eqs. (S41) and (S42), and eliminating $ds/dt$, we have

$$\tau_s \frac{ds}{dt} = \left\{ \frac{2\pi}{B} \left( \frac{2}{7} \right) P_0 - \frac{\tau_s}{\tau_d} \left[ 1 + \left( \frac{2}{3} \right) \xi \right] \right\} \epsilon_1. \tag{S43}$$

Hence the static bump remains stable when the coefficient of $\epsilon_1$ on the right hand side is non-positive. Using Eq. (S33) to eliminate $P_0$ and $\Pi/B$, we recover the condition in Eq. (24). This shows that the bump becomes a moving one as soon as the static bump becomes unstable against asymmetric fluctuations, as described in the main text.

Now we consider the stability of the moving bump. Eliminating $ds/dt$ and summarizing the equations in matrix form,

$$\tau_s \frac{d}{dt} \begin{pmatrix} \bar{u}_1 \\ \bar{e}_0 \\ \bar{e}_1 \end{pmatrix} = \begin{pmatrix} \frac{2}{B} - 1 & -\frac{a}{B} \xi & 0 \\ P_{0u} & P_{00} & -\frac{a}{B} \xi \\ P_{0u} & P_{00} & 0 \end{pmatrix} \begin{pmatrix} \bar{u}_1 \\ \bar{e}_0 \\ \bar{e}_1 \end{pmatrix}, \tag{S44}$$

where $P_{0u} = 2\rho_0 \tau_s / B \tau_d + \nu \tau_s \rho_1 / 2a \bar{u}$, $P_{00} = \nu \tau_s \rho_1 / 2\rho_0 - \frac{\bar{u}}{B \tau_s} \tau_d / B \rho_0 \tau_d$, and $P_{0u} = 2\rho_0 \tau_s / B \tau_d - \nu \tau_s \rho_1 / \alpha \bar{u}$. For the moving bump to be stable, the real parts of the eigenvalues of the stability matrix should be non-positive. The stable branches of the family of curves are shown in Fig. S2(a). The results show that the boundary of stability of the moving bumps is almost indistinguishable from the envelope of the family of curves. Higher order perturbations produce phase boundaries that have better agreement with simulation results, as shown in Fig. S2(b).

Fig. S2. (a) The stable branches of the family of the curves with constant values of $\xi$ at $\tau_d/\tau_s = 50$. The dashed line is the phase boundary of the static bump. (b) The boundary of the moving phase. Symbols: simulation results. Dashed line: 1st order perturbation. Solid line: 2nd order perturbation. Inset: The boundary of the moving phase in a broader range of $\beta$. Parameters: $N/L = 80/(2\pi)$, $a/L = 0.5/(2\pi)$.

E: Decoding in CANNs with STF

We start by considering bumps and STF profiles of the form

$$\Pi(x, t) = \Pi_0 \exp \left[ -\frac{(x - \xi_0 - s(t))^2}{4a^2} \right], \tag{S45}$$

$$f(x, t) = f_0 \exp \left[ -\frac{(x - \xi_0 - s(t))^2}{2a^2} \right] + f_1 \left( x - \xi_0 - s(t) \right) \exp \left[ -\frac{(x - \xi_0 - s(t))^2}{4a^2} \right]. \tag{S46}$$

Note that since the noise occurs in the position of the bump, we can neglect changes in the height. Substituting into Eq. 4, and removing terms orthogonal to the position distortion mode, we have

$$\tau_s \frac{d}{dt} \left( \hat{\xi} \right) = M \left( \hat{\xi} \right) + \frac{\lambda}{\tilde{a}_{0a}} \eta(t) \left( \begin{array}{c} 0 \\ -1 \end{array} \right). \tag{S47}$$

where

$$M = \left( \begin{array}{cc} \hat{\chi} & \left\{ \hat{\sigma}^{a \bar{a}} (\xi) \frac{\hat{\chi}}{\xi} + \frac{1}{\xi} \left[ 1 + \hat{\sigma}^{a \bar{a}} (\xi) \right] \right\} \\ -\left\{ \hat{\sigma}^{a \bar{a}} (\xi) \frac{\hat{\chi}}{\xi} + \frac{1}{\xi} \left[ 1 + \hat{\sigma}^{a \bar{a}} (\xi) \right] \right\} & -\left\{ \hat{\sigma}^{a \bar{a}} (\xi) \frac{\hat{\chi}}{\xi} + \frac{1}{\xi} \left[ 1 + \hat{\sigma}^{a \bar{a}} (\xi) \right] \right\} \end{array} \right). \tag{S48}$$

This differential equation can be solved by first diagonalizing $M$. Let $-\lambda_{\pm}$ be the eigenvalues of $M$, and $(U_{\pm} {^T} U_{\pm})^T$ be the corresponding eigenvectors. Then the solution becomes

$$\left( \begin{array}{c} \hat{\xi} \\ \hat{\epsilon} \end{array} \right) = \underbrace{\frac{\lambda}{\tilde{a}_{0a}} \int_{-\infty}^{t} dt_1 \eta(t_1) \left( \begin{array}{cc} E_+ & 0 \\ 0 & E_- \end{array} \right) U^{-1}}_{S49} \left( \begin{array}{c} 0 \\ -1 \end{array} \right),$$

where $E_{\pm} = \exp[-\lambda_{\pm}(t-t_1)]$. Squaring the expression of $\epsilon/a$, averaging over noise, and integrating,

$$\left\langle \left( \frac{\epsilon}{a} \right)^2 \right\rangle = 2T \left( \frac{\lambda}{\tilde{a}_{0a}} \right)^2 \sum_{a, b, \pm} \left\{ U_{aa} (U_{aa}^{-1} - U_{bb}^{-1}) \right\} \left( \frac{1}{(\lambda_a + \lambda_b)T_s} \right) U_{ab} \left( U_{aa}^{-1} - U_{bb}^{-1} \right). \tag{S50}$$

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