

Equivalency of spike-frequency and h-current-based adaptation in a Wilson-Cowan field model

Ronja Strömsdörfer^{1,2,*} and Klaus Obermayer^{1,2,3}

¹Neural Information Processing Group, Fakultät IV, Technische Universität Berlin, Berlin, Germany

²Einstein Center for Neuroscience, Berlin, Germany

³Bernstein Center for Computational Neuroscience, Berlin, Germany



(Received 17 October 2025; accepted 2 April 2026; published 26 June 2026)

During slow-wave sleep, the brain produces traveling waves of slow oscillations (SOs; ≤ 2 Hz), characterized by the propagation of alternating high- and low-activity states. They play a crucial role in memory consolidation and are frequently investigated, empirically and with the support of *in silico* studies. The question of internal mechanisms that modulate traveling waves of SOs is still unanswered even though it is established that it is an adaptation mechanism that mediates them. One of the main mechanisms investigated is spike-frequency adaptation, a hyperpolarizing feedback current that is activated during periods of high activity. An alternative mechanism that has recently been suggested is based on hyperpolarization-activated (h-)currents, which are positive feedback currents that are activated in low-activity states. Both adaptation mechanisms were shown to feature SO-like dynamics in neuronal populations, and the inclusion of a spatial domain seems to enhance observable differences in their effects. To investigate the effects of both adaptation mechanisms on the neural dynamics in detail, we examine a spatially extended, adaptive Wilson-Cowan model of interacting excitatory and inhibitory populations of neurons with local spatial coupling. The excitatory populations are equipped with either one or the other adaptation mechanism. We describe both mechanisms using the same dynamical equation and include the inverse mode of action by changing the signs of the adaptation strength and the gain of activation function. We then show that the dynamical systems including the two feedback currents are mathematically equivalent under a compensatory external input, which depends on the adaptation strength and which in turn leads to a shift in state space of the otherwise equivalent bifurcation structure. A detailed analysis of state space shows that strong enough adaptation is required to induce traveling waves of SO-like dynamics, while only stationary or homogeneous activity patterns emerge if adaptation is weak. Additionally, adaptation modulates the properties of the spatiotemporal activity patterns, such as temporal frequencies, spatial frequencies, and the speed of the traveling waves, all of which increase with increasing strength. Though being dynamically equivalent, our results also explain why location-dependent variations in feedback strength cause differences in the propagation of traveling waves between both adaptation mechanisms.

DOI: [10.1103/3sd6-d2w9](https://doi.org/10.1103/3sd6-d2w9)

I. INTRODUCTION

One of the most frequently investigated rhythms in the brain is the phenomenon of slow oscillations (SOs), which appear during slow-wave sleep and are characterized by the slow alternation of high- and low-activity states, also referred to as up- and down-states [1,2]. They were first described by Steriade *et al.* [3,4], and have been shown to play a crucial role in memory consolidation since then [6–8]. On a mesoscopic scale, SOs tend to travel in wavelike patterns across the cortex [9]. Due to their dominant temporal frequency being below ≤ 1 Hz, SOs are most likely driven by an adaptation process that acts on a slower timescale than the standard neuronal response. Nonetheless, the exact nature and dynamics of the adaptation mechanism are still in question.

One candidate process is spike-frequency adaptation (SFA), a hyperpolarizing feedback current (i.e., a negative feedback mechanism) induced by ongoing high activity in neuronal populations, which is often mediated by slow potassium (K^+) currents (see Refs. [10,11]). Since the neurotransmitter acetylcholine (ACh) decreases K^+ conductance [12] and since ACh concentration is lower during natural sleep compared to wakefulness [13], SFA is elevated during sleep. Comparing different species, two types of slow waves were separated in Ref. [14] depending on whether they occur in natural slow-wave sleep or whether they occur under anesthesia. Reference [15] reported that the durations of up-states following down-states are positively correlated during anesthesia in rats, while Ref. [14] observed a negative correlation, with long down-states being followed by short up-states in natural sleep in several species. In Ref. [14], reduced cholinergic modulation (i.e., lowered ACh concentration) increased the incidence of short up-states subsequent to long down-states, thereby recapitulating both the slow-wave patterns of natural sleep and the neuromodulatory effects of varying ACh concentrations in the sleeping brain. Hyperpolarization-activated h-currents (i.e., a positive feedback mechanism) have also been shown

*Contact author: stroemsdoerfer@tu-berlin.de

Published by the American Physical Society under the terms of the Creative Commons Attribution 4.0 International license. Further distribution of this work must maintain attribution to the author(s) and the published article's title, journal citation, and DOI.

to slowly modulate neuronal excitability (see Ref. [16]) and may also cause adaptation-driven traveling waves similar to cortical waves of SO-like dynamics. In Ref. [17], using ferret slice experiments, it was proposed that h-current modulation regulates the cortical capacity for recurrent persistent activity, which encompasses slow-wave dynamics. Until most recently, h-currents were predominantly investigated in thalamocortical systems [18–20], which aligns with their presence in thalamic neurons [21]. However, Refs. [22,23] focus on the impact of h-currents on cortical slow waves, i.e., on the propagation of alternating up- and down-states over space.

Spatially extended neural field models are a convenient computational approach for investigating the propagation features of traveling waves. They inherit a description of space through spatial convolution, which effectively describes distance-dependent connectivity profiles in continuous space [24–26]. Depending on their setup, neural field models can produce periodic traveling waves [27]. For the one-population model of integrate-and-fire neurons with synaptic inputs on a continuous one-dimensional space of Ref. [28], analytical predictions align with numerical simulations showing that the speed of traveling waves fluctuates over space when there is a subset of tightly coupled neurons. In Ref. [29], traveling waves emerge in a system of quadratic integrate-and-fire neurons with nonlocal synaptic coupling as the synaptic coupling strength is increased. Generally speaking, the emergence of spatiotemporal patterns relies on the underlying dynamical state of the model system. Suitable parametrizations can be identified by a Turing instability analysis performed in the Fourier domain. This analysis is most often performed in systems comprised of either a single neural population (e.g., Refs. [30,31]) or two coupled populations of excitatory and inhibitory neurons (e.g., Refs. [32,33]).

One frequently used model is the Wilson-Cowan model that was first introduced in Ref. [34] in its mass model version, i.e., without a spatial domain. The mass model version displays a rich variety of emergent dynamics and has previously been used to investigate SFA-driven SOs, either with [35,36] or without inhibition [37]. In its original form, comprising one excitatory and one inhibitory population of neurons without SFA [38], the dynamical landscape of this model remains fairly similar when both SFA and inhibition are included, when only SFA is present, or when both are absent. A regime of oscillations (e.g., emerging due to a Hopf instability) is at the corner end of a regime of bistability, where a stable up- and down-state coexist. Modified versions of the model have been constructed that include finer biophysical detail, e.g., synaptic plasticity, while maintaining the systems dimension at two differential equations as in Ref. [39], and the model has even found applications in the machine learning field [40].

To include a spatial domain, Wilson and Cowan extended the mass model to a field model that is comprised of two-coupled populations of excitatory and inhibitory neurons [41]. Pinto and Ermentrout [42] investigated the system without an inhibitory population, but with a linear, negative feedback that limits the networks excitability. They establish the existence of traveling pulses in such a network and connect the speed of the waves, which are induced by the slow negative feedback, to the model parameters using the Heaviside function as transfer function. For a homogeneous, excitatory neural

field model, Ref. [43] proved that lateral inhibition is required to stabilize bump solutions (i.e., stabilize the activity to not decay or vanish over time), and while Ref. [44] confirms these findings, they additionally show that local inhomogeneous input stabilizes stationary-pulse solutions in an otherwise homogeneous network. In Ref. [45], the authors investigate the same field model without inhibition in which nonlinear negative feedback to an excitatory population of neurons is produced by synaptic depression and SFA simultaneously. They identify traveling fronts and pulses, as well as stationary or homogeneous oscillations. They show that synaptic depression is not sufficient to stabilize bump solutions and confirm that either lateral inhibition (as shown in Ref. [43]) or external input (as shown in Ref. [44]) is required. Conversely, bumps do not exist when SFA is present. Their nonlinear formulation of SFA feedback is a physiologically based negative feedback. In Ref. [46], the authors equip the excitatory population of the two-population model with SFA and investigate the conditions for Turing and Hopf bifurcations to emerge, enabling stationary or spatiotemporal activity. While weaker and faster adaptation generates stationary patterns, slower and stronger adaptation causes the stationary patterns to travel.

Now, we are left with the question of what the differences are between the slow negative feedback mechanism based on SFA (see Refs. [36,47–51]) and the recently proposed positive feedback mechanism based on h-currents (see Refs. [22,23]) that have already been shown to induce SO-like dynamics. Simultaneous investigations of h-currents and SFA were already conducted. Reference [52] used fluorescent dye in the dentate gyrus of rats and unmodified versus blocked hyperpolarization-activated cyclic nucleotide-gated (HCN) channel [53] recordings to show that in the presence of HCN channels action potential (AP) initiation is enhanced during sustained firing and the propagation of AP patterns is sped up. They observe that in the presence of HCN channels, hyperpolarizing $\text{Na}^+\text{-K}^+$ currents are opposed. Reference [54] included both HCN (h-current-based adaptation) and M-channel (SFA) dynamics in a spiking neural network to investigate their role in seizure events in epilepsy patients. Reference [23] found, in slice experiments, that blocking h-currents results in prolonged up- and down-state durations, effectively decreasing the temporal oscillation frequency. With their computational model, they produce adaptation-driven SOs between up- and down-states where the implemented h-current- and SFA-based adaptation alternate in activation, depending on the membrane potential with h-currents active in down-, and inactive in up-states while the opposite is the case for SFA. With the model, they recreated the results found *in vitro*, prolonging up- and down-state durations, if the strength of h-currents is further reduced. Reference [22] tested whether a spatial gradient in excitability, degree of recurrent excitation, or strength of the SFA current would induce a sequential activation of cortical neurons (i.e., up-state onset) along the dorsoventral axis of the rat post-subiculum with a synchronous deactivation of the up-state. They observed this *in vivo* in naturally sleeping mice prior to their *in silico* experiments. Neither gradient was able to replicate the experimentally observed dynamics. Including h-currents with decreasing strength along the dorsoventral axis, on the other hand, reproduced their results. Although previous

studies examined each mechanism in detail, a unified investigation comparing both mechanisms, including systematic state space explorations, has not yet been performed.

To address this, we implement a Wilson-Cowan field model and consider two nonlinear adaptation mechanisms, a negative feedback mechanism induced by high neural activity and a positive feedback mechanism induced by low neural activity, capturing the most prominent features of SFA- vs h-current-based adaptation. The model is implemented on a one-dimensional spatial domain with periodic boundary conditions. Each location contains two interacting populations of excitatory and inhibitory neurons that are spatially coupled by a Gaussian synaptic connectivity kernel. The excitatory populations are locally equipped with either one of the two adaptation mechanisms. Since both mechanisms act in a functionally similar way, we describe them with the same dynamical equation and consider the inverse mode of action (negative vs positive feedback and activation during high- vs low-activity states) by changing the sign of the adaptation strength and the gain of the activation function. The model is parametrized to fulfill various criteria that have been shown to play a role in the formation of adaptation-driven slow waves, e.g., regimes of bistability (where stable up- and down-states coexist) in a cortical network for SOs during sleep [55] and anesthesia [56], or strong excitatory recurrence [57].

We first show that in our formulation both adaptation mechanisms are mathematically equivalent under a compensatory external input to the excitatory populations that depends on the adaptation strength. A state space analysis shows that strong enough adaptation is necessary to produce spatiotemporal activity patterns in this system that only generates homogeneous or stationary activity when adaptation is weak. Second, we conducted numerical simulations and show that in the two-population model the adaptation strength is a modulatory factor for the adaptation-driven slow waves. For the considered slices of state space, we observe an increase of dominant temporal frequencies, spatial frequencies, and travel speed of spatiotemporal activity patterns, the stronger the adaptation strength becomes. Numerical results agree with the results of the mathematical analysis performed before.

Due to the dynamical equivalence, the state spaces for the positive and negative feedback mechanisms are equal but shifted along the external input parameter of the excitatory population proportional to the adaptation strength. This finding may serve as a guideline for what differences to expect in a given neurobiological setting (e.g., when analyzing the effects of spatial gradients of adaptation strength as in Ref. [22]). Furthermore, the Wilson-Cowan field model with adaptation can serve as a reference when considering the influence of the additional differences in the physiological properties of SFA- and h-currents-based adaptation mechanisms.

II. THE SPATIALLY EXTENDED ADAPTIVE WILSON-COWAN MODEL

We use the original Wilson-Cowan continuum model of Ref. [41] with integro-differential equations (IDEs), including a convolution over a spatial domain, to investigate adaptation-driven traveling waves of SO-like dynamics. We include a third differential equation for an adaptation mechanism and

connect it to the excitatory population to describe the effects of either high-activity induced negative or low-activity induced positive feedback mechanisms. In the following, we refer to them as spike-frequency (*a*) or h-current (*h*)-mediated adaptation although the model is a simplification that focuses only on their most prominent biophysical features. The equations of the activities u_e and u_i of the excitatory and inhibitory populations and for the adaptation variable m are given by

$$\begin{aligned}\tau_e \frac{\partial}{\partial t} u_e(x, t) &= -u_e(x, t) + F_e(w_{ee}w_e(x) * u_e(x, t) \\ &\quad - w_{ei}w_i(x) * u_i(x, t) - bm(x, t) + I_e), \\ \tau_i \frac{\partial}{\partial t} u_i(x, t) &= -u_i(x, t) + F_i(w_{ie}w_e(x) * u_e(x, t) \\ &\quad - w_{ii}w_i(x) * u_i(x, t) + I_i), \\ \tau_m \frac{\partial}{\partial t} m(x, t) &= -m(x, t) + F_m(u_e(x, t) - \mu),\end{aligned}\quad (1)$$

where the spatial convolution is defined as

$$w_j(x) * u_j(x, t) = \int_{-\infty}^{\infty} w_j(|x - y|) u_j(y, t) dy, \quad j \in \{e, i\}.$$

The spatial kernel is given by the normalized (i.e., $\int_{-\infty}^{\infty} w_j(x) dx = 1$) Gaussian

$$w_j(|x - y|) = \frac{1}{\sqrt{2\pi}\sigma_j} e^{-\frac{|x-y|^2}{2\sigma_j^2}}, \quad (2)$$

with width σ_j , $j \in \{e, i\}$. The transfer functions are sigmoidal,

$$F_j(x) = \frac{1}{1 + e^{-\beta_j x}}, \quad j \in \{e, i, m\}. \quad (3)$$

The coupling strengths between the excitatory and inhibitory populations are given by connectivity weights w_{jl} , $j, l \in \{e, i\}$, in Eq. (1). The membrane time constants are designated with τ_j , $j \in \{e, i\}$. The adaptation mechanisms $m(x, t)$ are discussed in detail in Sec. II A; they are parametrized by a strength value b , a time constant τ_m , and a gain parameter β_m . Due to the transfer function in Eq. (3) being a sigmoid between zero and one, we interpret the activity variables u_e and u_i as the proportion of neurons firing per unit time [58]. Its gain parameter is denoted by β_j . The kernel widths in Eq. (2) determine the extent to which populations are effectively connected in space. Kernel widths are chosen to be smaller for excitatory and broader for inhibitory interactions, effectively implementing a Mexican-hat-shaped interaction between different locations. The parameters that are used in this study were adjusted such that adaptation-driven SOs are generated with an additional noisy external input (see Refs. [35, 49]), fast excitation-inhibition-driven oscillations can emerge (see Ref. [59]), and the system with and without adaptation shows regimes of bistability since this has been shown to play a crucial part in the formation of SOs (see Refs. [2, 55]).

The model is implemented as a one-dimensional neural field with periodic boundary conditions and a homogeneous connectivity profile. To reduce the effects of the finite size on the dynamics, we combine a large ring of length $L = 600$ with comparably small widths σ_j , $j \in \{e, i\}$, of the spatial kernels. The ring is discretized into n positions, each of which is

TABLE I. List of model parameters. The abbreviations “exc” and “inh” stand for “excitatory population” and “inhibitory population,” respectively.

Parameter	Value	Description
μ_e	0	Excitatory threshold
μ_i	0	Inhibitory threshold
β_e	5	Excitatory gain
β_i	5	Inhibitory gain
w_{ee}	3.2	Coupling strength exc to exc
w_{ei}	2.6	Coupling strength inh to exc
w_{ie}	3.3	Coupling strength exc to inh
w_{ii}	0.9	Coupling strength inh to inh
I_e	$[-2.5, 2]$	External input current to exc
I_i	$[-3.5, 1]$	External input current to inh
τ_e	10	Membrane time constant of exc
τ_i	15	Membrane time constant of inh
σ_e	1	Spatial spread of exc
σ_i	3	Spatial spread of inh
μ	0.3	Adaptation threshold
dx	0.3	Integration space step
L	600	Length (circumference) of ring
b	$[0, 1]$	SFA strength
τ_m	300	SFA time constant
β_m	10	SFA gain
$-b$	$[0, 1]$	H-current strength
τ_m	300	H-current time constant
$-\beta_m$	10	H-current gain

equipped with a node whose dynamics is described by Eq. (1). Therefore, the integration space step is given by $dx = \frac{L}{n}$.

A. The adaptation mechanisms

The excitatory populations are equipped with an adaptation mechanism, generally understood as a process (not restricted to the brain) that modulates the effect of a sustained input but acts on a slower timescale (see Ref. [60]). In the following, we distinguish two adaptation processes caused by different types of somatic conductances in cortical neurons (see Ref. [61]). SFA, a negative feedback mechanism, is mediated by slow potassium currents that activate when the activity of the excitatory population is high. This causes a hyperpolarizing feedback current that effectively inhibits the neural response of excitatory neurons (see Ref. [50]). H-current-based adaptation is mediated by hyperpolarization-activated nucleotide-gated channels (see Ref. [62]), which open if the excitatory population is in a low-activity state and return positive feedback, i.e., effectively excite the excitatory population. Functionally, the adaptation mechanisms are similar (see Ref. [63] for SFA, for h-currents, see Ref. [64] where the authors discuss h-currents in thalamic neurons, and see Refs. [22,61] for both adaptation mechanisms in cortical neurons), so that we can describe their main effects by the same differential equation (last equation in Eq. (1); see Ref. [22]) and include the inverse mode of action (positive versus negative feedback,

activated during high- versus low-activity values) by changing the sign of the parameters for adaptation strength b and adaptation gain β_m . Parameters are summarized in Table I.

B. Fixed points and stability analysis of the model with adaptation

To determine the fixed points we consider a single Wilson-Cowan node. Due to the normalization of the kernel, its fixed points are equivalent to the fixed points of the spatially extended model. Let $\frac{\partial u_e}{\partial t} = \frac{\partial u_i}{\partial t} = 0$ in Eq. (1). From $\frac{\partial m}{\partial t} = 0$, we obtain $m = F_m(u_e - \mu)$, which we insert in the equation for the excitatory population. The nullclines $f(u_e)$ and $g(u_i)$ are then given by

$$u_i = f(u_e) = \frac{1}{w_{ei}}(w_{ee}u_e + I_e - bF_m(u_e - \mu) - F_e^{-1}(u_e)),$$

$$u_e = g(u_i) = \frac{1}{w_{ie}}(w_{ii}u_i - I_i + F_i^{-1}(u_i)).$$

A point $(\tilde{u}_e, \tilde{u}_i, \tilde{m}) \in (0, 1)^3$ is a fixed point if $f(\tilde{u}_e) = \tilde{u}_i$, $g(\tilde{u}_i) = \tilde{u}_e$, and $F_m(\tilde{u}_e - \mu) = \tilde{m}$.

We apply the procedure from Wyller *et al.* [33,65], Harris and Ermentrout [32,66], and Byrne *et al.* [67] to investigate the stability of the homogeneous steady states (i.e., the fixed points) of field models. To do so, we add a small spatial perturbation to the homogeneous steady state,

$$u_e(x, t) = \tilde{u}_e + \chi(x, t),$$

$$u_i(x, t) = \tilde{u}_i + \varphi(x, t),$$

$$m(x, t) = \tilde{m} + \phi(x, t). \quad (4)$$

Then, we insert Eq. (4) into Eq. (1) and linearize the system around the homogeneous steady state by applying a Taylor expansion up to the first order in $\chi(x, t)$, $\varphi(x, t)$, and $\phi(x, t)$. We obtain

$$\tau_e \partial_t \chi = -\chi + w_{ee}F'_e(B_e)w_e * \chi - w_{ei}F'_e(B_e)w_i * \varphi - bF'_e(B_e)\phi,$$

$$\tau_i \partial_t \varphi = -\varphi + w_{ie}F'_i(B_i)w_e * \chi - w_{ii}F'_i(B_i)w_i * \varphi,$$

$$\tau_m \partial_t \phi = -\phi + F'_m(\tilde{u}_e - \mu)\chi,$$

where $B_e := w_{ee}\tilde{u}_e - w_{ei}\tilde{u}_i - bF_m(\tilde{u}_e - \mu) + I_e$ and $B_i := w_{ie}\tilde{u}_e - w_{ii}\tilde{u}_i + I_i$. The zero-order terms vanish for $\tilde{u}_e$ and $\tilde{u}_i$, because the spatial kernels are normalized to one. To transform this set of integro-differential equations (IDEs) into a set of ordinary differential equations (ODEs), we exploit the fact that a convolution in the spatial domain is a product in the frequency domain [i.e., $w(x) * \chi(x, t) = \hat{w}(k)\hat{\chi}(k, t)$, where $\hat{\cdot}$ denotes the Fourier transformation]. This leads to the ODE system

$$\tau_e \partial_t \hat{\chi} = -\hat{\chi} + w_{ee}F'_e(B_e)\hat{w}_e \hat{\chi} - w_{ei}F'_e(B_e)\hat{w}_i \hat{\varphi} - bF'_e(B_e)\hat{\phi},$$

$$\tau_i \partial_t \hat{\varphi} = -\hat{\varphi} + w_{ie}F'_i(B_i)\hat{w}_e \hat{\chi} - w_{ii}F'_i(B_i)\hat{w}_i \hat{\varphi},$$

$$\tau_m \partial_t \hat{\phi} = -\hat{\phi} + F'_m(\tilde{u}_e - \mu)\hat{\chi}. \quad (5)$$

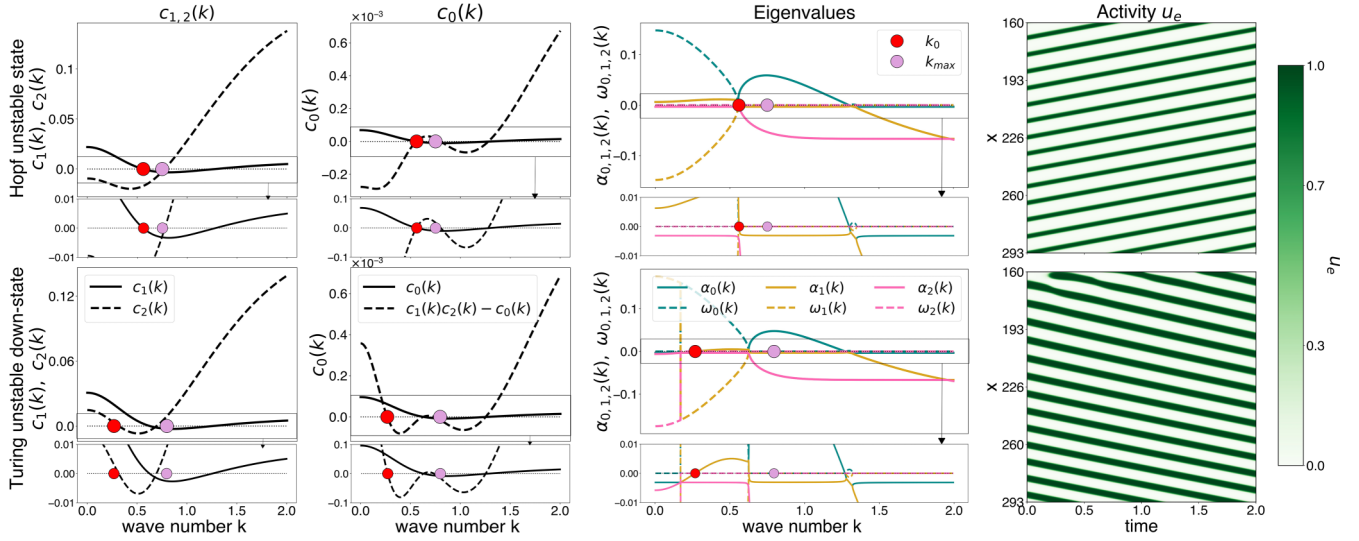


FIG. 1. Examples for static (top row) and dynamic (bottom row) Turing instabilities in a Hopf- (top row) and Turing-unstable state (bottom row) for the system with h-currents. Panels from left to right show [cf. Eq. (7)]: Coefficients $c_1(k)$ (solid line) and $c_2(k)$ (dashed line), coefficient $c_0(k)$ (solid line) and condition $c_1(k)c_2(k) - c_0(k)$ (dashed line), real $[\alpha_{0,1,2}(k)$, solid lines] and imaginary $[\omega_{0,1,2}(k)$, dashed lines] parts of the eigenvalues of the linearization matrix, and the corresponding activity pattern $u_e(x, t)$. Circles denote the wave numbers k_0 (red) and $k_{\max}$ (pink) (see text). Insets below each plot show close-ups of the thin boxes. Values for the external input currents and the adaptation parameter were $(I_e, I_i) = (-0.7, -0.6)$, $b = -0.5$ (top row) and $(I_e, I_i) = (-0.3, -0.3)$, $b = -0.5$ (bottom row). All other parameters are given in Table I.

For $\vec{X} = \begin{pmatrix} \hat{x} \\ \hat{\phi} \end{pmatrix}$, Eq. (5) can be written in vector notation, $\partial_t \vec{X} = A_3(k) \vec{X}$, where

$$A_3(k) = \begin{bmatrix} -\frac{1}{\tau_e} + \frac{w_{ee} F'_e(B_e) \hat{w}_e(k)}{\tau_e} & -\frac{w_{ei} F'_e(B_e) \hat{w}_i(k)}{\tau_e} & -\frac{b}{\tau_e} F'_e(B_e) \\ \frac{w_{ie} F'_i(B_i) \hat{w}_e(k)}{\tau_i} & -\frac{1}{\tau_i} - \frac{w_{ii} F'_i(B_i) \hat{w}_i(k)}{\tau_i} & 0 \\ \frac{F'_m(\tilde{u}_e)}{\tau_m} & 0 & -\frac{1}{\tau_m} \end{bmatrix} =: \begin{bmatrix} a_{11}(k) & a_{12}(k) & a_{13} \\ a_{21}(k) & a_{22}(k) & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}, \quad (6)$$

$B_e := w_{ee} \tilde{u}_e - w_{ei} \tilde{u}_i - b F_m(\tilde{u}_e - \mu) + I_e$, and $B_i := w_{ie} \tilde{u}_e - w_{ii} \tilde{u}_i + I_i$. The stability of the fixed point can be characterized by the eigenvalues $\lambda_j(k) = \alpha_j(k) + i\omega_j(k)$, $j \in \{0, 1, 2\}$, of the linearization matrix (Jacobian) $A_3(k)$, where i denotes the imaginary unit. The eigenvalues correspond to the roots of the cubic polynomial

$$\begin{aligned} \det(A_3(k) - \lambda \mathbf{I}) &= \lambda^3 + \lambda^2(-(a_{11}(k) + a_{22}(k) + a_{33})) + \lambda(a_{11}(k)a_{22}(k) + a_{11}(k)a_{33} + a_{22}(k)a_{33} - a_{13}a_{31} - a_{12}(k)a_{21}(k)) \\ &\quad + (-a_{11}(k)a_{22}(k)a_{33} + a_{22}(k)a_{13}a_{31} + a_{33}a_{12}(k)a_{21}(k)) \\ &= \lambda^3 + \lambda^2 c_2(k) + \lambda c_1(k) + c_0(k), \end{aligned}$$

with

$$\begin{aligned} c_0(k) &= -a_{11}(k)a_{22}(k)a_{33} + a_{22}(k)a_{13}a_{31} \\ &\quad + a_{33}a_{12}(k)a_{21}(k), \\ c_1(k) &= a_{11}(k)a_{22}(k) + a_{11}(k)a_{33} + a_{22}(k)a_{33} \\ &\quad - a_{13}a_{31} - a_{12}(k)a_{21}(k), \\ c_2(k) &= -(a_{11}(k) + a_{22}(k) + a_{33}). \end{aligned} \quad (7)$$

Fixed points with $\alpha_j(k) < 0$ for all $j \in \{0, 1, 2\}$ are stable.

Instabilities of homogeneous equilibria

In the following, we investigate the stability of homogeneous equilibria in analogy to Ref. [33]. If the model system, for a fixed parametrization, has a fixed point that is unstable at $k = 0$ [i.e., $\alpha_j(0) \geq 0$ for at least one $j \in \{0, 1, 2\}$; see Fig. 1,

first row], we call the fixed point *Hopf unstable*, if $\omega_j(0) \neq 0$, or simply *unstable*, if $\omega_j(0) = 0$.

A fixed point $(\tilde{u}_e, \tilde{u}_i, \tilde{m})$ corresponds to a generalized Turing situation at $k_0 > 0$ if $c_0(k_0) = 0$, i.e., if one of the eigenvalues is zero for this wave number. This is illustrated in Fig. 1, first row, where the condition is met for the wave number k_0 indicated by the red circle. The instability occurring at k_0 can also be called static [68]. If $c_2(k_0)c_1(k_0) - c_0(k_0) = 0$ for $c_1(k_0) > 0$, i.e., if one eigenvalue at this wave number is purely imaginary, the fixed point corresponds to a finite bandwidth instability with oscillations (also called dynamic [68] or a Turing-Hopf instability; see Ref. [67]). This is illustrated in Fig. 1, second row, where the condition is met, for example, for the wave number indicated by the red marker. Since all bands of unstable modes are of finite width (see Appendix A 1), at least two zero crossings occur for some

$k_1 > k_0 > 0$, if the fixed point displays a Turing instability. If both types (i.e., static and dynamic) of Turing situations occur, it is called a mixed Turing situation. We refer to a fixed point that is stable at $k = 0$ for which a static, dynamic, or mixed Turing situation occurs, under the umbrella term “*Turing unstable*.” For the investigated parametrizations, Hopf-unstable states may also have bands of unstable modes at nonzero wave numbers $k > 0$ (see, e.g., Fig. 1, first row).

Since we are particularly interested in adaptation-driven slow alternations between high- (up) and low-activity (down) states, we distinguish up- ($\tilde{u}_e \geq 0.3$) from down- ($\tilde{u}_e < 0.3$) by the fixed point value of the excitatory population. Consequently, when a Turing instability emerges in an up- (down-) state, we call the state *Turing-unstable up- (down-) state*. In addition, the model exhibits regimes of bistability between two fixed points where stable up- and down-states coexist for the same location in state space. If either one of the two states loses stability for some $k_0 > 0$ due to an emerging Turing situation while the coexisting fixed point remains stable, we call the Turing-unstable state a *Turing-unstable up- or down-state in bi*, respectively.

Note that there is a difference in the instability of modes between Hopf-unstable states with bands of unstable modes

with nonzero wave numbers $k > 0$ and other Turing-unstable states, which is exemplified in Fig. 1, third column (Eigenvalues). In Hopf-unstable states, unstable modes already occur for wave number values $0 \leq k \leq k_0$, while in Turing-unstable states, the minimum wave number for unstable modes is $k_0 > 0$.

C. Wave numbers

If a fixed point is identified as Turing- or Hopf unstable, we compute the smallest wave number $k_0 > 0$ at which the conditions for one of the abovementioned Turing instabilities are fulfilled. Examples are shown in Fig. 1, where k_0 is marked by the red circles. Additionally, we determine the wave number $k_{\max}$ (see pink circles in Fig. 1) for which the corresponding unstable mode grows most rapidly, i.e., for which the real part $\alpha_j(k)$ of the largest eigenvalue becomes maximal, $k_{\max} = \operatorname{argmax}_k(\max_j \alpha_j(k))$.

D. Symmetries and equivalence of mechanisms

Let Eq. (1),

$$S(u_e, u_i, m) = \begin{pmatrix} \tau_e \frac{\partial u_e}{\partial t} \\ \tau_i \frac{\partial u_i}{\partial t} \\ \tau_m \frac{\partial m}{\partial t} \end{pmatrix} = \begin{pmatrix} -u_e(x, t) + F_e(w_{ee}w_e(x) * u_e(x, t) - w_{ei}w_i(x) * u_i(x, t) - bm(x, t) + I_e) \\ -u_i(x, t) + F_i(w_{ie}w_e(x) * u_e(x, t) - w_{ii}w_i(x) * u_i(x, t) + I_i) \\ -m(x, t) + F_m(u_e(x, t) - \mu) \end{pmatrix}, \quad (8)$$

be the system with SFA (i.e., let $b, \beta_m > 0$), and let $T : [0, 1]^3 \rightarrow [0, 1]^3$, with

$$T : (u_e, u_i, m)^\top \mapsto (u_e, u_i, 1 - m)^\top,$$

be an isomorphic transformation. Then, we have $\frac{\partial}{\partial t}[T((u_e(x, t), u_i(x, t), m(x, t))^\top)] = (\frac{\partial u_e}{\partial t}, \frac{\partial u_i}{\partial t}, -\frac{\partial m}{\partial t})^\top$. Inserting the transformation into Eq. (8), we obtain

$$\begin{aligned} S(\mathbf{T}(\mathbf{u}_e, \mathbf{u}_i, \mathbf{m})) &= \begin{pmatrix} \tau_e \frac{\partial u_e}{\partial t} \\ \tau_i \frac{\partial u_i}{\partial t} \\ -\tau_m \frac{\partial \mathbf{m}}{\partial \mathbf{t}} \end{pmatrix} = \begin{pmatrix} -u_e(x, t) + F_e(w_{ee}w_e(x) * u_e(x, t) - w_{ei}w_i(x) * u_i(x, t) - \mathbf{b}(1 - \mathbf{m}(\mathbf{x}, \mathbf{t})) + I_e) \\ -u_i(x, t) + F_i(w_{ie}w_e(x) * u_e(x, t) - w_{ii}w_i(x) * u_i(x, t) + I_i) \\ -(-(1 - \mathbf{m}(\mathbf{x}, \mathbf{t})) + \underbrace{F_m(u_e(x, t) - \mu)}_{=1 - F_m(\mu - u_e)}) \end{pmatrix} \\ &= \begin{pmatrix} -u_e(x, t) + F_e(w_{ee}w_e(x) * u_e(x, t) - w_{ei}w_i(x) * u_i(x, t) + bm(x, t) - b + I_e) \\ -u_i(x, t) + F_i(w_{ie}w_e(x) * u_e(x, t) - w_{ii}w_i(x) * u_i(x, t) + I_i) \\ -m(x, t) + F_m(\mu - u_e(x, t)) \end{pmatrix}. \end{aligned}$$

This system of equations is, given the choice of F_m [Eq. (3)], equivalent to the system of Eq. (1) for h-currents if $-b \leftarrow b$ and $-\beta_m \leftarrow \beta_m$ (see Table I) and the external input to the excitatory population in the system with SFA is decreased by the value of b , i.e., $I_e^h = I_e^a - b$. The superscripts a and h indicate the difference between the variables and parameters for SFA and h-currents, respectively. Hence, both adaptation mechanisms are dynamically equivalent under the transformation T , if I_e is correspondingly changed and if $F_m^a(x) = 1 - F_m^h(x)$ holds for the adaptation nonlinearity. This equivalence also tells us that a fixed point $(\tilde{u}_e^a, \tilde{u}_i^a, \tilde{m}^a)$ for the system with SFA corresponds to a fixed point $(\tilde{u}_e^h, \tilde{u}_i^h, 1 - \tilde{m}^h)$ for the system with h-currents and that the dynamical landscape for h-currents should be the same as the dynamical landscape for SFA, but shifted along the I_e axis by the value b .

Beyond dynamical equivalence between the adaptation mechanisms, we also have a symmetry for each system within itself. Let $T : [0, 1]^3 \rightarrow [0, 1]^3$ with $T : (u_e, u_i, m)^\top \mapsto (1 - u_e, 1 - u_i, 1 - m)^\top$ be another isomorphic transformation such

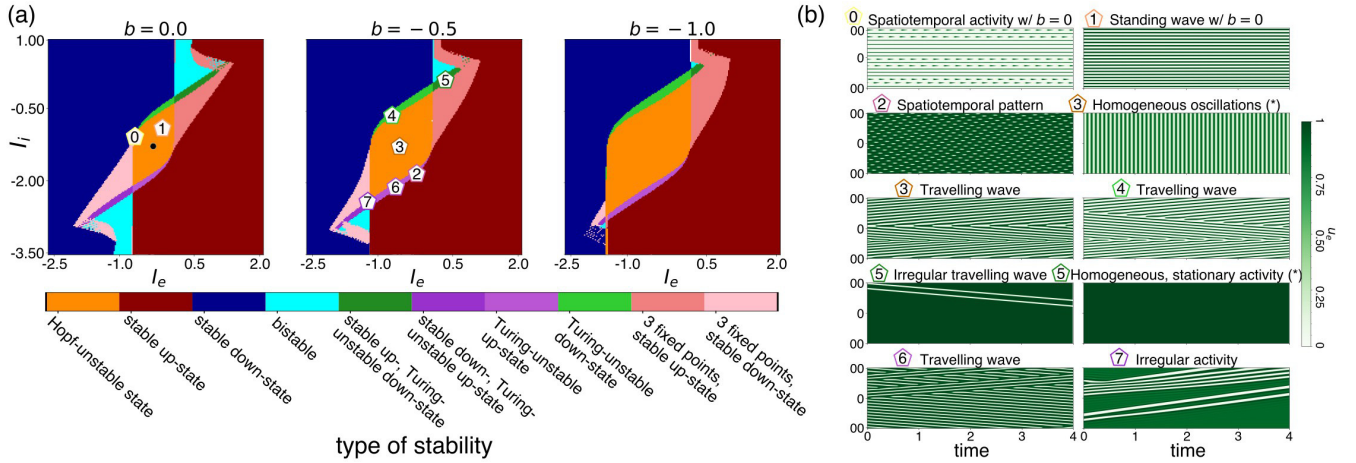


FIG. 2. State spaces and activity patterns for the Wilson-Cowan model with h-currents. (a) Results of the stability analyses for a slice of parameter space spanned by the external input currents $(I_e, I_i) \in [-2.5, 2] \times [-3.5, 1]$ for increasing adaptation strength $|b| \in \{0, 0.5, 1.0\}$ (left to right). Colors denote the different dynamical regimes (see legend). Pentagon markers identify the positions in state space corresponding to the activity traces shown in panel (b). Resolution of state space is 181×181 . The black dot in the state space for $b = 0$ denotes center of point symmetry (see Sec. II D). (b) Activity traces $u_e(x, t)$ for different locations in state space (see Table II), denoted by pentagons in panel (a). Two types of bistability are exemplified in panels 3, 3(*) and 5, 5(*) (see text). Lighter green denotes low-activity values and darker green denotes high-activity values (see color bar). All simulations were initialized around their corresponding fixed points, except for the activity traces marked with (*), which were initialized close to zero (see Appendix B 1).

that $\frac{\partial}{\partial t} [T((u_e(x, t), u_i(x, t), m(x, t))^T)] = (-\frac{\partial u_e}{\partial t}, -\frac{\partial u_i}{\partial t}, -\frac{\partial m}{\partial t})^T$. Inserting this in Eq. (8), we obtain

$$\begin{pmatrix} -\tau_e \frac{\partial u_e}{\partial t} \\ -\tau_i \frac{\partial u_i}{\partial t} \\ -\tau_m \frac{\partial m}{\partial t} \end{pmatrix} = \begin{pmatrix} 1 - u_e(x, t) - F_e(w_{ee}w_e(x) * (1 - u_e(x, t)) - w_{ei}w_i(x) * (1 - u_i(x, t)) - b(1 - m(x, t)) + I_e) \\ 1 - u_i(x, t) - F_i(w_{ie}w_e(x) * (1 - u_e(x, t)) - w_{ii}w_i(x) * (1 - u_i(x, t)) + I_i) \\ 1 - m(x, t) - F_m((1 - u_e(x, t)) - \mu) \end{pmatrix} \\ = \begin{pmatrix} -u_e(x, t) + F_e(w_{ee}w_e(x) * u_e(x, t) - w_{ei}w_i(x) * u_i(x, t) - bm(x, t) - I_e - w_{ee} + w_{ei} + b) \\ -u_i(x, t) + F_i(w_{ie}w_e(x) * u_e(x, t) - w_{ii}w_i(x) * u_i(x, t) - I_i - w_{ie} + w_{ii}) \\ -m(x, t) + F_m(u_e(x, t) + \mu - 1) \end{pmatrix}. \quad (9)$$

If $\hat{I}_e = -I_e + b - w_{ee} + w_{ei}$, $\hat{I}_i = -I_i - w_{ie} + w_{ii}$, and $\hat{\mu} = 1 - \mu$, then the system (9) is equivalent to Eq. (1) for both SFA and h-currents. This induces an approximate point symmetry of state space at $(I_e^c, I_i^c) = (\frac{b - w_{ee} + w_{ei}}{2}, \frac{-w_{ie} + w_{ii}}{2})$ between (u_e, u_i, m) and $(1 - u_e, 1 - u_i, 1 - m)$, which becomes exact for $\mu = 0.5$. Since $\mu = 0.3$ in this study, an exact symmetry is only achieved for $b = 0$ [Fig. 2(a), first column, where the black dot in the middle of the orange regime denotes the center of the point reflection].

III. OVERVIEW OF STATE SPACE AND ITS CHANGES WITH ADAPTATION STRENGTH

Figure 2 shows the results of the analytical investigation for the system with h-currents with increasing adaptation

TABLE II. Input pairs (I_e, I_i) for Fig. 2.

Location	0	1	2	3	4	5	6
I_e	-0.65	0	-0.05	-0.5	-0.55	0.4	-0.55
I_i	-1	-0.75	-1.6	-1.25	-0.425	0.2	-2

strength [Fig. 2(a)] and examples for the emerging spatiotemporal patterns [Fig. 2(b)] for all regimes of Hopf or Turing instability. Without adaptation ($b = 0$), we observe a Hopf-unstable regime (orange) in which both temporal [similar to Fig. 2(b), panel 3(*), for $b = -0.5$] and spatial [see Fig. 2(b), panel 1] patterns emerge. With adaptation, the Hopf regime is also apparent but the activity patterns can be either temporal [Fig. 2(b), panel 3(*)] or spatiotemporal [Fig. 2(b), panel 3]. Close to the boundaries of the Hopf-unstable regime, we observe the emergence of Turing instability in down-states [upper border; for an activity example, see Fig. 2(b), panel 4] and in up-states [lower border; for activity example, see Fig. 2(b), panel 6]. Beyond the Turing instability in down- (up-) states, to the left (right) side of the state spaces in Fig. 2(a), there exists a regime, marked dark blue (dark red), where a single down- (up-) state fixed point is stable. We also see regimes of three fixed points including one stable up-state (dark beige), while the other two fixed points are unstable and vice versa with one stable down-state (light beige). Activity traces in these regimes are similar to the activities shown in Fig. 2(b), panels 5(*) and 7. Initializations close to zero always converge to the existing stable fixed point

while initializations around the unstable states cause irregular traveling waves. Further, to both corner ends (upper right and lower left), we find a regime of bistability between up- and down-states (light blue) next to regimes, where a stable down-state coexists with a Turing instability in the up-state (dark purple) and vice versa (dark green). Figure 2(b), panel 5, shows that the activity converges to the activity caused by the Turing instability in the down-state, if initialized close to the Turing-unstable down-state. Initialized close to zero, the activity converges to the stable up-state [see activity 5(*)]. The pattern emerging in the Turing-unstable down-state of panel 5 shows down-state waves traveling over an otherwise stable up-state activity, unlike the traveling waves shown in panels 4 and 6, where no other stable fixed point coexists. Furthermore, in some states, the activity patterns can become irregular [see Fig. 2(b), panel 7], such that they do not converge to a periodic, equidistant, or otherwise regular pattern. Such irregular patterns predominantly occur at the border of different regimes or in states where another attractor, e.g., a stable fixed point, coexists.

The Hopf-unstable states further experience spatial instability for some $k > 0$ (see, for example, Fig. 1, top row, third panel), giving rise to spatial (for $b = 0$, static Turing instability) or spatiotemporal (for $b \neq 0$, dynamic Turing instability) patterns. Initialized close to the fixed points, states in the Hopf regime converge to spatial or spatiotemporal patterns, while other initializations, e.g., initializations close to zero, converge to fast, spatially homogeneous, temporal oscillations (see also Appendix B 2). In this regime, the system thus experiences a second type of bi- (or potentially multi-) stability that is not caused by the coexistence of multiple fixed points. However, there are two small areas in the Hopf-unstable regime for $b = 0$, where exceptions occur and where spatiotemporal patterns are present [Fig. 2(b), panel 0]. These areas are located in the top left of the Hopf regime where a stable down-state, three fixed points with a stable down-state, a Hopf instability, and a Turing instability are getting close in parameter space, and in the bottom right corner, where the regimes of a stable up-state, a Hopf instability, three fixed points with a stable up-state, and a Turing instability meet. In these states, depending on the initialization, most of the ring converges toward the standing wave interspersed by a few traveling bumps [see Fig. 2(b), panel 0]. When adaptation strength increases, the regimes of bistability between two stable fixed points (light blue) shrink and vanish for values $|b| > 1$. The size of the Hopf-unstable regime (orange) and of the regime of three fixed points with a stable up-state (beige) increases, while the regime of three fixed points with a stable down-state decreases in size (light beige).

Figure 3 shows a comparison between the state spaces and activity traces for the systems with SFA and h-currents. We see in Fig. 3(a) that the dynamical regimes are equivalent for SFA (left) and h-currents (right), except for the shift to the right (left) by the absolute value $|b|$ for SFA (h-currents), consistent with the required compensation of external inputs to the excitatory population (see Sec. IID). The rightward shift of the dynamical regimes for SFA compared to h-currents implies that the system requires more external input to the excitatory population to produce activity patterns beyond the spatially and temporally homogeneous steady states. We

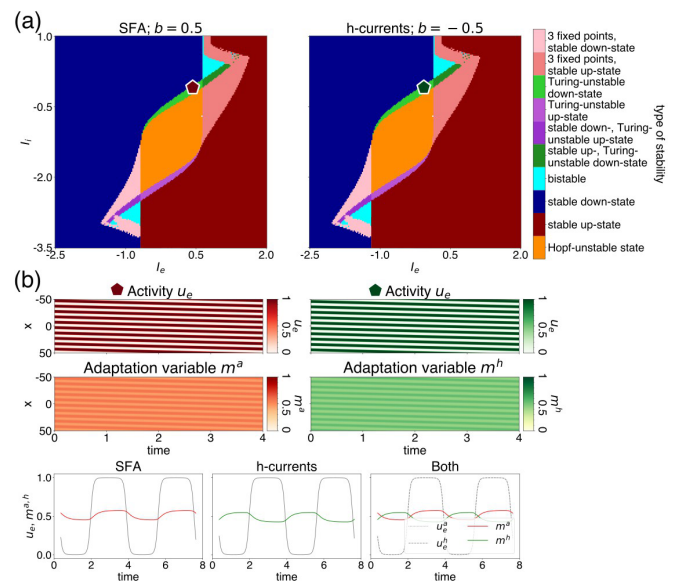


FIG. 3. Comparison of state spaces and activity patterns for both adaptation mechanisms. (a) Slices of state space for SFA (left) and h-currents (right) for $|b| = 0.5$ spanned by the external input currents I_e and I_i . Colors denote the different dynamical regimes (see legend). Colored pentagon markers identify the positions in state space corresponding to the activity traces shown in panel (b). The external input currents are $(I_e, I_i) = (0.4, -0.3)$ for SFA and $(I_e, I_i) = (-0.1, -0.3)$ for h-currents. (b) Top row: Activity traces $u_e(x, t)$ for the locations in state space, marked in panel (a). Middle row: Corresponding traces of the adaptation variable m . Bottom row: Activity traces and traces of the corresponding adaptation variable for a fixed spatial location for the traveling waves shown above for SFA (left panel) and h-currents (middle panel). All traces are superimposed in the right panel.

also see that equivalent positions (considering the required compensatory inputs) cause activity patterns to be equivalent under the transformation T , i.e., for $m \leftarrow 1 - m$, as exemplified in Fig. 3(b).

For the investigated parametrization (see Table I), adaptation is required to cause the purely temporal or spatial patterns observed at $b = 0$ to travel. We exemplify this in Fig. 4, where we show the real $[\alpha_j(k)]$ and imaginary $[\omega_j(k)]$ parts of all three eigenvalues $\lambda_j(k) = \alpha_j(k) \pm i\omega_j(k)$ of the Jacobian [Eq. (6)] for a Hopf-unstable (upper row) and a Turing-unstable (center and bottom row) state. In the upper two rows, for small values of b , the zero crossings of the real parts of any eigenvalue coincide with nonzero imaginary parts, resulting in a dynamic Turing instability and enabling spatiotemporal patterns in that very state. For $b = 0$, the imaginary part vanishes, resulting in a static Turing instability. However, adaptation cannot be arbitrarily weak and must be stronger than some threshold to show a dynamic Turing instability. In the bottom row of Fig. 4, for example, the Turing instability is static for $b = -0.02$ and $b = -0.01$, allowing the system to produce standing waves (see Appendix A 3, Fig. 8). While the Turing instability at k_0 becomes dynamic for $b = -0.03$, all eigenvalues have negative real parts for $b = -0.02$ for every k for which the imaginary part is nonzero.

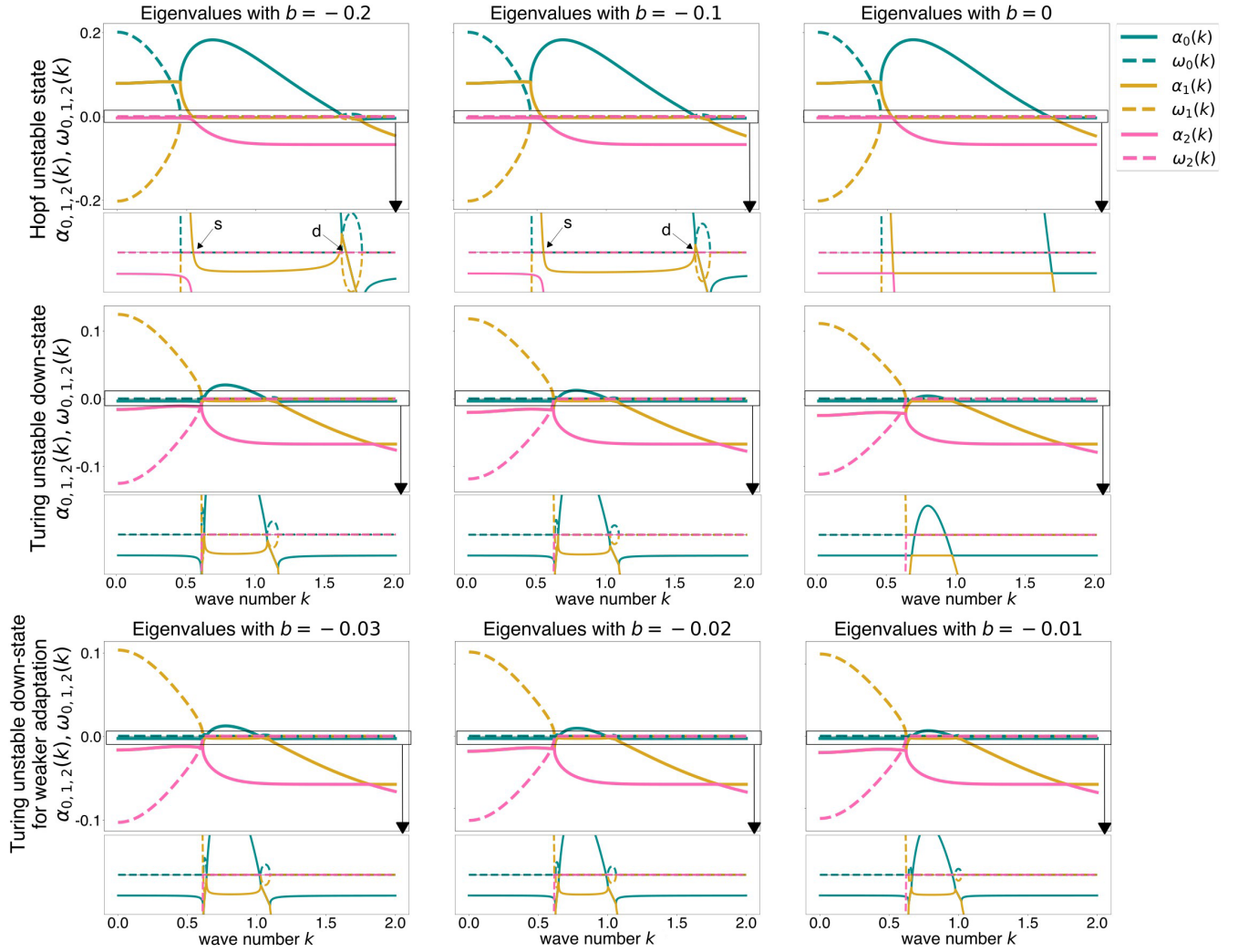


FIG. 4. Eigenvalue spectrum for small values of $|b|$. The panels show the real, $\alpha_{0,1,2}(k)$, (solid lines) and imaginary parts, $\omega_{0,1,2}(k)$, (dashed lines) of the eigenvalues of the linearization matrix in Eq. (6). Top row: Hopf-unstable state at $(I_e, I_i) = (-0.35, -1.225)$. Center row: Turing-unstable down-state at $(I_e, I_i) = (-0.35, -0.55)$. Bottom row: same Turing-unstable down-state as in the center row but with weaker adaptation. Adaptation strength $|b|$ decreases from left to right. Lower panels show close-ups around the zero crossing of the real parts. The imaginary parts vanish for $b = 0$. Arrows in panels below the first two plots of the upper row indicate zero crossing of a static (s) and dynamic (d) Turing instability.

Additionally, we see in Fig. 4, as $|b|$ increases, the imaginary part becomes larger, which indicates faster temporal oscillations, since each mode is given by

$$\begin{aligned} \exp(\lambda(k)t) \exp(ikx) &= \exp(\underbrace{(\alpha(k) \pm i\omega(k))}_{=0}) \exp(ikx) \\ &= \exp(\underbrace{\pm i\omega(k)t}_{\omega \uparrow \text{ for } |b| \uparrow}) \exp(ikx). \end{aligned}$$

Above conclusions are confirmed for the entire slices of state space in Appendix A 2 (Fig. 7).

IV. CHARACTERIZATION OF REGULAR SPATIOTEMPORAL PATTERNS IN HOPF- AND TURING-UNSTABLE STATES

Figure 5 shows the results of the numerical investigation for the system with h-currents with increasing adaptation strength for the regimes of Hopf or Turing instability, where

regular patterns occur. We did not consider the regimes of three fixed points [corresponding to dark and light beige in Fig. 2(a)], because numerical simulations close to the fixed points undergoing a Turing instability lead to irregular propagation of activity fronts similar to the pattern exemplified in Fig. 2(b), panel 7, which shows irregular activity emerging in a Turing-unstable up-state in bi.

Figure 5(a) shows the wave number $k_{\max}$ (top row), the spatial frequency multiplied to the length of the ring, $L \cdot f_x$ (center row, effectively describing the number of bumps on the ring), and temporal frequency, f_t (bottom row) of the emerging patterns for different locations in state space and for increasing adaptation strength. $k_{\max}$ values vary continuously across state space. Values are larger than 0.44 with highest values occurring in Turing-unstable states (see color bar). The spatial frequency of the wave patterns changes smoothly across state space for $b = 0$ with the highest values occurring toward the center of the Hopf regime. Values

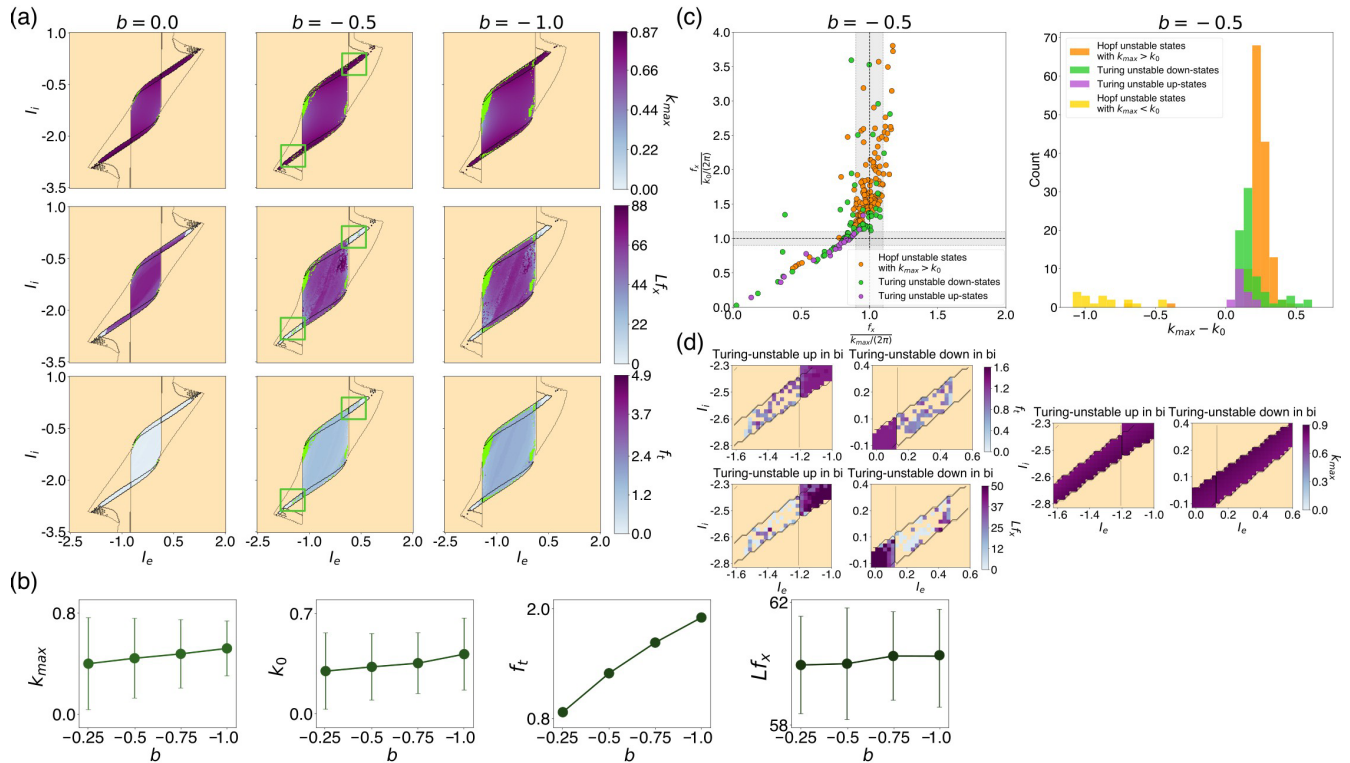


FIG. 5. Properties of the spatiotemporal patterns emerging in Hopf- and Turing-unstable states for increasing h-current strength. (a) $k_{\max}$ values (top row), number $L \cdot f_x$ of bumps on the ring (middle row), and dominant temporal frequency f_t (bottom row) for each location in state space. The figure shows slices of state space spanned by the external input $(I_e, I_i) \in [-2.5, 2] \times [-3.5, 1]$ for $b \in \{0, -0.5, -1.0\}$. Purple colors denote the corresponding feature values. Darker colors indicate higher values (see color bar). Yellow denotes states of no spatiotemporal activity; light green denotes states with irregular patterns with a standard deviation r of the Kuramoto-order parameter of $r > 10^{-2}$. Thin lines denote the boundaries of the dynamical regimes shown in Fig. 2(a). Green boxes correspond to the panels shown in panel (d). (b) Mean (dots) and variance (bars) of $k_{\max}$, k_0 , f_t , and $L \cdot f_x$ for $b \in \{-0.25, -0.5, -0.75, -1\}$ for the states located in the Hopf-unstable, Turing-unstable up-, and Turing-unstable down-state regimes, for regular spatiotemporal activity for which the standard deviation of the Kuramoto-order parameter over time and space was $r \leq 10^{-2}$ (see Appendix B 4). (c) Left: Scatter plot of the ratios between the spatial frequency f_x of the emerging patterns and the spatial frequencies corresponding to the wave numbers k_0 and $k_{\max}$ for all locations in state space from panel (a) with $b = -0.5$, which were identified as Hopf-unstable states with $k_{\max} \geq k_0$ (orange), Turing-unstable down- (purple), or Turing-unstable up-states (green). Perfect agreement with a given mode corresponds to a ratio of 1 (vertical and horizontal dashed lines). The gray regions around each ratio being 1 denote deviations smaller than 10%. Right: Distribution of the differences $k_{\max} - k_0$ for the same state space, additionally including the Hopf-unstable states with $k_{\max} < k_0$. (d) Close-ups of state space [see green boxes in panel (a)] with values for $k_{\max}$ (right), $L \cdot f_x$ (lower left), and f_t (upper left) in the Turing-unstable up- (left panels) and down-states (right panels) in bi. Yellow denotes states of no spatiotemporal activity or with irregular patterns with a standard deviation r of the Kuramoto-order parameter of $r > 10^{-2}$. The other colors denote feature values (see color bars). Wave numbers were acquired as described in Sec. II B; spatial and temporal frequencies as described in the Appendixes B 1 and B 3. Numerical simulations were conducted with initialization close to the corresponding unstable fixed points.

decrease toward the borders. For $b = -0.5$ and $b = -1$, the distribution of $L \cdot f_x$ becomes less smooth with nonequidistant, irregular patterns ($r > 10^{-2}$) emerging toward the borders of the Hopf regime, where the regimes of Turing instability, one stable fixed point, Hopf instability, and three fixed points with only one stable state meet [green areas inside instability regimes; Fig. 5(a)]. The numerical simulations also confirm that the activity traces for $b = 0$ are stationary spatial waves, as f_t is zero. For adaptation strong enough, waves start moving resulting in a finite value of f_t , which increases with the value of $|b|$ [see also Fig. 5(b)] confirming what is expected from the mathematical analysis. For increasing $|b|$, the averages of the wave numbers k_0 and $k_{\max}$ increase in value, albeit the variance over state space is high. f_x increases with $|b|$ consistent with the increase of the wave numbers k_0 and

$k_{\max}$. Additionally, the average temporal frequency increases steeply, which is expected from the increasing imaginary parts at the zero crossings of the real parts of the eigenvalues as discussed in Sec. III.

Figure 5(c), right panel, shows the distribution of the differences $k_{\max} - k_0$. The case, $k_{\max} - k_0 < 0$, occurs only in locations with fixed points identified as Hopf unstable and where irregular activity patterns emerge. Figure 5(c), left panel, shows the ratio between the simulated spatial frequencies and the wave numbers k_0 and $k_{\max}$ plotted against each other. Perfect agreement between f_x and a wave number k would be indicated by the corresponding point falling onto the horizontal or vertical line of the ratios being 1. All activity patterns emerging from locations in state space with $k_{\max} < k_0$ are irregular and are not considered in the comparison to f_x .

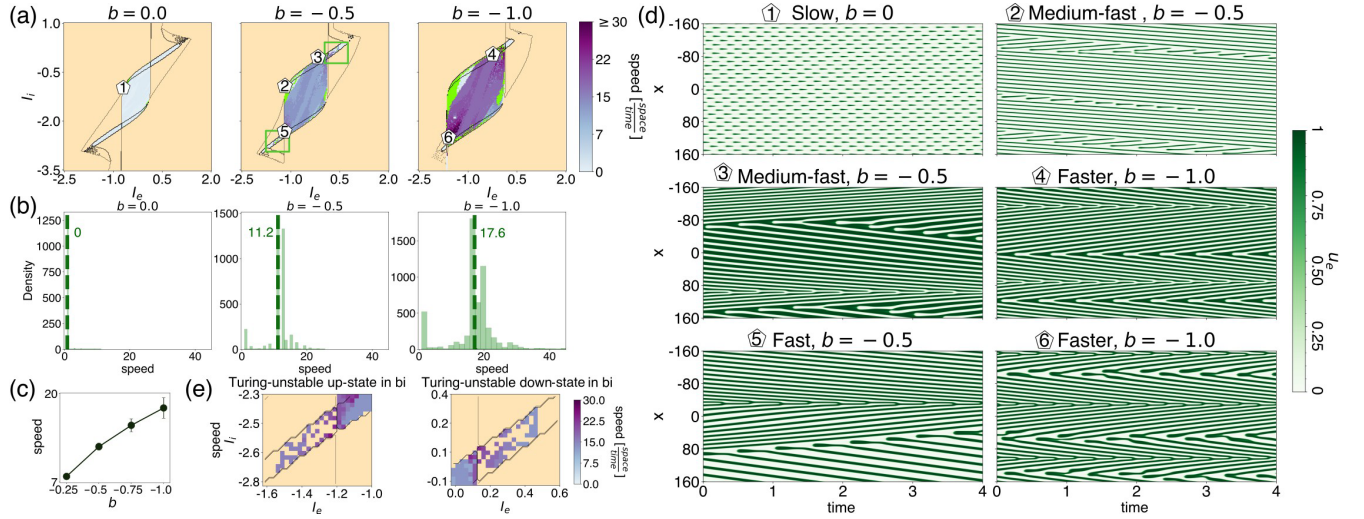


FIG. 6. Propagation speed of spatiotemporal patterns emerging in Hopf- and Turing-unstable states for increasing adaptation strength. (a) Slices of state space spanned by the external input currents showing speed values for the corresponding location in state space. Adaptation strength increases from left to right. Speed values are indicated by purple (see color bar), yellow denotes states of no spatiotemporal activity, and green denotes states of irregular patterns with $r > 10^{-2}$. Thin lines denote the borders of the dynamical regimes shown in Fig. 2(a). (b) Histograms of the distribution of speed values across the states shown in panel (a). Dashed vertical lines and numbers denote the location of the peaks of the histograms. (c) Average (dots) and variance (bars) of speed values across state space for $b \in \{-0.25, -0.5, -0.75, -1.0\}$. (d) Spatiotemporal patterns of $u_e(x, t)$ for different values of b emerging in the locations in state space that are indicated by hexagons in panel (a). The corresponding value of the external input currents is given in Table III. The corresponding speed values are for 1: < 0.5 ; 2 and 3: 11.6; 4: 17.7; 5: 14.6; 6: 18.7. All other parameters are given in Table I. (e) Close-ups of state spaces [see green boxes in Fig. 6(a)] with values for speed. Numerical simulations were initialized around the fixed points of Hopf or Turing instability. Speed values were computed as described in Appendix B 5.

The gray regions around each ratio being 1 denote deviations smaller than 10%. Since $k_{\max}$ denotes the strongest growing unstable mode (compare Sec. II C), one would expect points to lie close to the vertical line in the center (for which $\frac{f_x}{k_{\max}/(2\pi)}$ is close to one), which is indeed the case. However, some exceptions for Turing-unstable up- and down-states occur.

Since we observe bistability in Hopf-unstable states between spatially homogeneous oscillations and temporally stationary spatial oscillations (see Sec. III), we performed the same analysis as in Figs. 5(a) and 5(c), but initialized close to zero. Results are similar and shown in Appendix B 6 (Fig. 10). This figure also shows the k_0 values over slices of state space corresponding to Fig. 5(a).

Figure 5(d) shows close-ups of Turing unstable up- and down-states in bi for $b = -0.5$. $k_{\max}$ values do not deviate strongly from the $k_{\max}$ values of the rest of the considered state spaces but only few numerical simulations converged to regular spatiotemporal patterns (nonyellow locations in the close-ups of state space). The resulting patterns strongly depend on the initialization, and even initializations close to the Turing-unstable fixed point do not necessarily converge to a regular spatiotemporal pattern but to the coexisting stable fixed point, as exemplified in Fig. 2(b), panel 5(*), or irregular patterns [69], as exemplified in Fig. 2(b), panel 7. If regular spatiotemporal patterns emerge, traveling waves show low values of spatial frequency. Temporal frequencies are also lower compared to the rest of state space. To determine the propagation speed of adaptation-driven waves, we computed the phase velocity as described in Appendix B 5 for each spatiotemporal activity pattern emerging in Turing-

or Hopf-unstable states. Figure 6(a) shows the absolute value of the velocity, i.e., the *speed* for different locations in state space and for $b \in \{0.0, -0.5, -1.0\}$. Speed values increase, the larger $|b|$ becomes. Toward the border of the regime of Hopf instability at which multiple different instability regimes meet (e.g., see region around hexagons 1 and 2), the activity patterns are either not regular (i.e., $r > 10^{-2}$) or not spatiotemporal (e.g., purely spatial). Toward the regions of Turing instability in bi, speed increases (e.g., see darker colors around hexagon 6).

Figure 6(b) shows the distribution of speed values across Hopf-unstable and Turing-unstable states. The stronger the adaptation, the higher the speed values are. For $b = 0$, as expected, activity patterns do not travel across space (recall Fig. 2, panel 0) or their speed is < 0.5 [see Fig. 6(d), panel 1]. For $b = -0.5$, there are two different speed values appearing the most often, with the dominant speed being 11.2. For $b = -1$, the variance of the distribution is larger and the most common speed value is once again higher at 17.6. Figure 6(c) confirms that the average speed across state space increases with adaptation strength. Figure 6(d) shows traveling waves for the same relative locations in state space (i.e., consid-

TABLE III. Input pairs (I_e, I_i) for Fig. 6.

Location	1	2	3	4	5	6
I_e	-0.6	-0.85	-0.025	-0.275	-1.1	-1.35
I_i	-0.875	-0.875	-0.2	-0.2	-2.325	-2.325

ering the shift to the left discussed in Sec. III), increasing in adaptation strength from left to right column. “Broad” patterns become “narrower,” increasing both temporal and spatial frequencies and their slope in the space-time diagrams, henceforth, the speed.

Figure 6(e) shows the same close-ups as Fig. 5(d) of Turing-unstable up- and down-states in bi, showing the speed values for the numerical simulations converging to regular traveling waves. Speed values tend to be higher closer to the boundary of the regimes of single Turing-unstable up- and down-states.

V. DISCUSSION

We implemented the adaptive Wilson-Cowan field model in a homogeneous setting with local connectivity on a one-dimensional spatial domain and periodic boundary conditions. Each position on the ring consists of an excitatory and an inhibitory population of neurons. The excitatory population is equipped with an adaptation mechanism that either corresponds to a hyperpolarizing negative feedback current (SFA) or a hyperpolarization-activated positive feedback current (h-currents). The parametrization used throughout this study was chosen to display multiple different phenomena that are also observed in the brain—from excitation-inhibition-driven faster oscillations, regimes of bistability, to spatiotemporal activity patterns that show SO-like dynamics as either adaptation mechanism is active.

We investigated the model system for increasing adaptation strength $|b|$, although the adaptation time constant τ_m has an effect on the temporal dynamics of adaptation-driven traveling waves as well. The larger τ_m , the lower the dominant temporal frequency becomes (results not shown, but see Ref. [47]), as has also been observed experimentally (see Ref. [70]). Changing the time constant scales the eigenvalues for the different parametrizations explored. This has no effect on the shape and size of the (in)stability regions, but can influence the properties of the zero crossing (i.e., whether the root at k_0 is real or whether it has a nonzero imaginary part) and the type of the emerging activity patterns (i.e., stationary vs spatiotemporal, results not shown). This is consistent with Ref. [46] that showed that for a reduced system, τ_m determines whether a Turing bifurcation is dynamic or static. A semianalytical stability analysis across parameter space was performed for increasing adaptation strength, resulting in the identification of over ten dynamical regimes. These included regimes of bistability between two stable fixed points and a regime that admits bistability (or potentially multistability) between different activity patterns depending on the initialization. The dynamical landscape exhibits parallels with the models studied in Refs. [35–38], but our analysis additionally displays regimes with Turing-unstable states, which are located at the border of regimes exhibiting oscillatory activity or a bistability between two fixed points. Spatiotemporal patterns, most often periodic adaptation-driven traveling waves, emerge in states exhibiting Hopf and Turing instabilities if adaptation is sufficiently strong. Activity patterns remain stationary in the absence of adaptation, which is explained by the zero imaginary part of all eigenvalues of the linearization matrix when a fixed point displays a Turing instability. This

aligns with the results presented in Ref. [46], which proved the existence of stationary patterns for the reduced system when adaptation was sufficiently weak, while traveling waves occurred for stronger adaptation.

Changing the adaptation strength not only alters the model’s dynamical regimes but also the features of the emerging temporal and spatial patterns including the speed of traveling wave activity. The numerical simulations aligned with the mathematical analysis performed before. With stronger adaptation, wave numbers increase on average, causing more waves on the ring, i.e., higher dominant spatial frequencies. Analogously, with growing imaginary parts of the eigenvalues at the zero crossing of their respective real parts for stronger adaptation, temporal frequencies also increase. These changes correlate with increasing traveling speeds of activity patterns when the adaptation becomes stronger. In our two-population model, adaptation is a modulatory factor for spatiotemporal patterns, contrary to the purely excitatory model with synaptic depression of Ref. [45].

Our results also show that the two adaptation mechanisms are mathematically equivalent when adaptation strength is compensated by a changed external input current. This is not a contradiction to the results of Ref. [22], who investigated SFA versus h-currents experimentally and using computational modeling. They identified differences between SFA and h-currents induced slow sequences of synchronized neuronal activity and sequential state transitions between up- and down-states. While a spatial gradient in the adaptation strength for SFA caused sequential down-state onsets and synchronized up-state onsets, h-currents replicated experimentally observed synchronized down-state onsets and sequential up-state initiation. Here, we show that the adaptation strength b has to be compensated by an additional external input to the excitatory population to preserve equivalency all the while adaptation induces and governs the emergent spatiotemporal properties. Consequently, a spatially heterogeneous adaptation strength [i.e., $b \rightsquigarrow b(x)$] will shape the emergent spatiotemporal activity patterns over space and break the equivalence between SFA and h-currents unless it is compensated by a spatially dependent external input $I_e \rightsquigarrow I_e(x)$.

In our population-based model, both adaptation mechanisms were implemented in a simplified way. Hyperpolarizing feedback current of somatic SFA can be mediated by potassium channels, which activate when the excitatory neurons are in a depolarized high-activity state, effectively causing K^+ outward flow [12,71]. Different potassium channels have different properties leading to differential effects in the actual adaptation mechanism: Voltage- (I_m ; see Ref. [72]) and sodium-activated K^+ channels (I_{KNa} ; see Ref. [73]) contribute mostly to subthreshold, while Ca^{2+} -activated K^+ channels (I_{KCa} [74]) contribute to spike-based adaptation. Different channel types also have different effects on the response properties of a neuron, for example, on a neuron’s f-I curve when adaptation strength is increased [50]. In addition, SFA can be mediated by sodium current inactivation that causes the excited population of neurons to become less depolarized via the inactivation of Na^+ inward flow [75]. That said, our SFA model appropriately captures their canonical role as slow, hyperpolarizing feedback mechanisms that activate

in an up-state. H-current-based adaptation is mediated by a different channel dynamics, causing dichotomous effects. The responsible HCN channels cause K^+ outward flow, all the while not preventing Na^+ inward flow [76], and have a reversal potential between -50 and -20 mV [16]. Unlike potassium channels that have a clear selection of K^+ (see Ref. [77]), HCN channels have a permeability of 3:1 to 5:1 for $K^+ : Na^+$ [16,78,79]. HCN channels are active as long as the neurons conductance is close to its resting membrane potential, causing positive inward currents that effectively excite the neuron. This, we simulate here, whereas the stagnating inhibitive effect for higher values of the membrane potential is neglected, similar to the cortical population model of Ref. [22]. Clearly, dynamical equivalence between SFA and h-current-based adaptation is only expected to strictly hold for the approximate description of the adaptation dynamics given by Eqs. (1) and (3).

For the reason of particularly addressing the influence of the dichotomy of the most prominent features of the adaptation mechanisms, we omitted delays, although it has been shown that delays can drive directions of waves in oscillator networks (see Ref. [80]) and enrich the emergent dynamics of complex spatiotemporal patterns (see Ref. [81]). Delays, however, would not affect the shown symmetry of the adaptation mechanisms.

Traveling waves of SOs are often presented as the propagation of alternating up- and down-states (see Refs. [2,37]), in which one can separate the propagation of up-states via down-to-up transitions from the traveling of down-states via up-to-down transitions. In our model, we show that h-currents require less external input to the excitatory population than SFA to transition from a maintained stable down-state into oscillatory states, due to the shift of state space to the left along the I_e axis. Note that even though we conduct simulations in a parameter space spanning negative values for external input currents, including thresholds in the transfer functions of the neuronal populations shifts the state space, exactly as is, along the axes of the external input currents by the value of the thresholds.

In the mean-field model with SFA of Ref. [48], the authors show that SFA shifts the state space horizontally to the right along the axis of the external input to the excitatory population, which agrees with our results. Consequently, to simulate a maintained up-state activity that, either by transient or noisy inputs, allows temporal deactivation of the neuronal populations into a down-state (i.e., down-state onsets), requires more external input to the excitatory population. Additionally, we see in our state spaces that the opposite holds for h-currents, induced by the shift to the left. H-currents consequently require less external input both for up-state onsets as well as down-state onsets, and therefore, also lower transient inputs to maintain a slow alternation between up- and down-states.

Further studies could extend our investigations to a biophysically more realistic model, for example, as in Ref. [50], which distinguishes subthreshold activated versus spike-triggered SFA. Reference [47] shows that for the model of Ref. [50], subthreshold-activated SFA changes the neuronal input-output relationship, and can increase the variability of interspike intervals (ISIs) independent of current inputs, whereas spike-triggered SFA changes the ISIs variability

based on the input to the neurons. It would be interesting to see how far the diverse types of activations in SFA would break the shown symmetry to h-current-based adaptation. For both adaptation mechanisms, the work of Refs. [23,82] for nonspatial conductance-based models would allow to simulate other potentially symmetry-breaking channel dynamics, e.g., the stagnating inhibitive effect of h-currents. The Wilson-Cowan model investigated in this study may serve as a reference when exploring the effects of a biophysically realistic channel dynamics.

ACKNOWLEDGMENTS

We thank Prof. Tilo Schwalger (Technische Universität Berlin) for very helpful comments and discussions. This work was funded by the Deutsche Forschungsgemeinschaft (DFG) as part of the CRC 1315 (Project No. 327654276).

DATA AVAILABILITY

The data that support the findings of this article are openly available [84]; embargo periods may apply.

APPENDIX A

1. Finite bandwidth of unstable modes

The eigenvalues depend on the Fourier transform of the spatial kernel $w_j(x)$ $j \in \{e, i\}$ [Eq. (2)], which is a normalized Gaussian in the real domain. In the Fourier domain, it has its maximum magnitude at 0 with $|\hat{w}_j(0)| = 1$, and its amplitude $|\hat{w}_j(k)|$ decays to zero for $k \rightarrow \infty$. Furthermore, the dynamical system is well defined, since the sigmoidal transfer functions [Eq. (3)] restrict the state variables always to the range between $[0, 1]$, and their derivatives are bounded functions. As long as the time constants τ_j , $j \in \{e, i, m\}$, are nonzero, the eigenvalues remain finite for any wave number k . Infinitely sized bands of unstable modes cannot exist because the Jacobian matrix

$$A_3(k) = \begin{bmatrix} -\frac{1}{\tau_e} + \frac{w_{ee}}{\tau_e} F'_e(B_e) \hat{w}_e(k) & -\frac{w_{ei}}{\tau_e} F'_e(B_e) \hat{w}_i(k) & -\frac{b}{\tau_e} F'_e(B_e) \\ \frac{w_{ie}}{\tau_i} F'_i(B_i) \hat{w}_e(k) & -\frac{1}{\tau_i} - \frac{w_{ii}}{\tau_i} F'_i(B_i) \hat{w}_i(k) & 0 \\ \frac{F'_m(\tilde{u}_e - \mu)}{\tau_m} & 0 & -\frac{1}{\tau_m} \end{bmatrix} \\ \rightarrow \begin{bmatrix} -\frac{1}{\tau_e} & 0 & -\frac{b}{\tau_e} F'_e(B_e) \\ 0 & -\frac{1}{\tau_i} & 0 \\ \frac{F'_m(\tilde{u}_e - \mu)}{\tau_m} & 0 & -\frac{1}{\tau_m} \end{bmatrix}, \quad \text{for } k \rightarrow \infty,$$

has always eigenvalues with negative real parts in the long wavelength limit. The coefficients of the characteristic polynomial become

$$c_0 = \frac{1 + b F'_m(\tilde{u}_e - \mu) F'_e(B_e)}{\tau_e \tau_i \tau_m}, \\ c_1 = \left(\frac{1}{\tau_e \tau_i} + \frac{1}{\tau_i \tau_m} + \frac{1 + b F'_m(\tilde{u}_e - \mu) F'_e(B_e)}{\tau_e \tau_m} \right), \\ c_2 = \frac{1}{\tau_e} + \frac{1}{\tau_i} + \frac{1}{\tau_m},$$

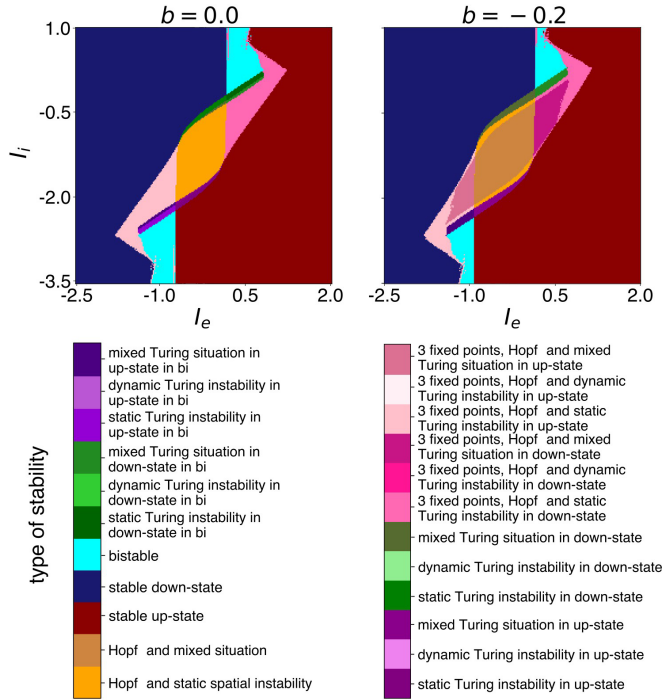


FIG. 7. State spaces over input pairs $(I_e, I_i) \in [-2.5, 2] \times [-3.5, 1]$ for $b \in \{0, -0.2\}$. Colors denote the different types of instability and the corresponding fixed point in which they occur (see color bar).

where $(\tilde{u}_e, \tilde{u}_i, \tilde{m})$ denotes a fixed point and B_e is defined as for Eq. (6). Since $b \cdot F'_m(\tilde{u}_e - \mu) > 0$ for both the SFA and the h-current settings, we have $c_0, c_1, c_2 > 0$. Furthermore,

$$c_2 c_1 - c_0 = \underbrace{\left(\frac{1}{\tau_e} + \frac{1}{\tau_m} \right)}_{>0} \underbrace{\left(\frac{1}{\tau_e \tau_i} + \frac{1}{\tau_i \tau_m} \right)}_{>0} + \underbrace{\frac{1 + b F'_m(\tilde{u}_e - \mu) F'_e(B_e)}{\tau_e \tau_m}}_{>0} + \underbrace{\frac{1}{\tau_e \tau_i^2} + \frac{1}{\tau_i^2 \tau_m}}_{>0} > 0.$$

As a consequence of the Routh-Hurwitz stability criterion, all eigenvalues of the Jacobian matrix in the small wavelength limit have negative real parts. Therefore, all bands of unstable modes are of finite bandwidth.

2. Slices of state spaces for small values of b

Figure 7 shows the state spaces for $b = 0$ and $b = -0.2$ including the distinction of static vs dynamic Turing instability. Without adaptation, the system shows static Turing instabilities only. For weak adaptation ($b = -0.2$), nearly all states formerly exhibiting a static Turing instability display either a dynamic Turing instability or a mixed Turing situation.

3. Activity traces for traveling and standing waves with finite adaptation

Figure 8 shows the excitatory activity for very weak adaptation. While for $b = -0.03$, the waves travel over space, they become stationary for $b = -0.02$.

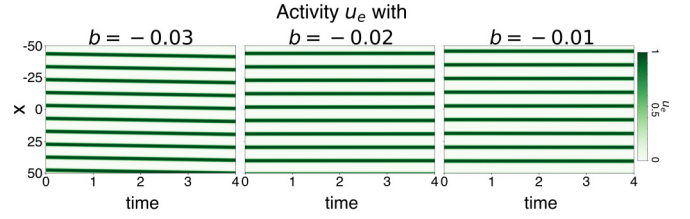


FIG. 8. Activity traces $u_e(x, t)$ corresponding to the Turing-unstable down-state shown in Fig. 4, bottom row, for $x \in [-50, 50]$.

APPENDIX B: NUMERICAL SIMULATIONS AND FEATURE ACQUISITION

1. Initialization and implementation

All models are implemented in Python. The code is provided at [83,84]. Within this framework, notebooks generating Figs. 1 and 4 are provided, allowing users to enlarge figures for a more detailed view. The temporal integration is implemented using Runge-Kutta of the fourth order with an integration time step $dt = 0.1$. For the spatial convolution, we used the Fourier transform of numpy. For every parametrization, we conducted numerical simulations with two different initializations in fixed points that were either Hopf- or Turing unstable. For random initialization, we sampled $u_e(x, 0), u_i(x, 0), m(x, 0)$, for every position x on the ring, from a uniform distribution $\mathcal{U}(0, 0.001)$. When initializing close to the fixed point value $(\tilde{u}_e, \tilde{u}_i, \tilde{m})$, additive noise was sampled from a normal distribution with standard deviation 0.1. For the latter, we conducted three simulations with three different seeds to ensure that all results presented in this study were not an artefact of the particular seed used. All features (temporal and spatial frequencies, regularity, and speed of spatiotemporal patterns) that were investigated were computed for the excitatory activity traces u_e . We conducted numerical simulations with a duration of 30 time units and discarded the first 10 time units to reduce the effects of transients.

2. Robustness of numerical methods and model dynamics

Fixed points were computed numerically at each location in state space using the Python function `scipy.optimize.root()` with more than 60 different initial conditions. All found fixed points $(\tilde{u}_e, \tilde{u}_i, \tilde{m})$ satisfied the root conditions [i.e., Eq. (8); $\mathcal{S}(\tilde{u}_e, \tilde{u}_i, \tilde{m}) = \vec{0}$] within an absolute tolerance of $< 10^{-8}$. Stability was determined from analytically derived Jacobian matrices.

To assess the robustness of the stability analysis, eigenvalues were recomputed after perturbing each fixed point by $\xi = 10^{-8}$, i.e., $(\tilde{u}_e + \xi, \tilde{u}_i + \xi, F'_m(\tilde{u}_e + \xi - \mu))$ and $(\tilde{u}_e - \xi, \tilde{u}_i - \xi, F'_m(\tilde{u}_e - \xi - \mu))$. The real part of the dominant eigenvalue, $\max_j(\text{real}(\lambda_j(k)))$, $j \in \{0, 1, 2\}$, determines the stability of a mode k . We now separately consider the modes $k = 0$ and $k > 0$. To identify whether the stability of a fixed point is correctly identified at $k = 0$, or for some $k > 0$, we computed

$$M_0(u_e, u_i, m) = \max_j(\text{real}(\lambda_j(0))),$$

$$M(u_e, u_i, m) = \max_{j,k}(\text{real}(\lambda_j(k))),$$

for the fixed point and their perturbed values to then collect the minimum and maximum, i.e.,

$$\begin{aligned} \min(M_0) &= \min\{M_0(\tilde{u}_e, \tilde{u}_i, F_m(\tilde{u}_e - \mu)), M_0(\tilde{u}_e + \xi, \tilde{u}_i + \xi, F_m(\tilde{u}_e + \xi - \mu)), M_0(\tilde{u}_e - \xi, \tilde{u}_i - \xi, F_m(\tilde{u}_e - \xi - \mu))\}, \\ \max(M_0) &= \max\{M_0(\tilde{u}_e, \tilde{u}_i, F_m(\tilde{u}_e - \mu)), M_0(\tilde{u}_e + \xi, \tilde{u}_i + \xi, F_m(\tilde{u}_e + \xi - \mu)), M_0(\tilde{u}_e - \xi, \tilde{u}_i - \xi, F_m(\tilde{u}_e - \xi - \mu))\}, \\ \min(M) &= \min\{M(\tilde{u}_e, \tilde{u}_i, F_m(\tilde{u}_e - \mu)), M(\tilde{u}_e + \xi, \tilde{u}_i + \xi, F_m(\tilde{u}_e + \xi - \mu)), M(\tilde{u}_e - \xi, \tilde{u}_i - \xi, F_m(\tilde{u}_e - \xi - \mu))\}, \\ \max(M) &= \max\{M(\tilde{u}_e, \tilde{u}_i, F_m(\tilde{u}_e - \mu)), M(\tilde{u}_e + \xi, \tilde{u}_i + \xi, F_m(\tilde{u}_e + \xi - \mu)), M(\tilde{u}_e - \xi, \tilde{u}_i - \xi, F_m(\tilde{u}_e - \xi - \mu))\}. \end{aligned}$$

If $\min(M)$, $\max(M) < 0$, the fixed point is classified as stable. Vice versa, if $\min(M)$, $\max(M) > 0$, the fixed point is classified as unstable. Finally, if $\min(M) < 0$ and $\max(M) > 0$, the classification would be ambiguous. This case most likely occurs in locations in state space that are close to a bifurcation. We found that for all locations inside the instability regions that we evaluated, $\min(M) > 0$ was fulfilled with a minimum at $7.8 \times 10^{-6} > 0$. We found the same for $\min(M_0)$ for all evaluated locations in state space inside the regime of Hopf instability. This implies that at all representative locations in state space for which we performed the stability analysis, the corresponding fixed points were robustly classified as unstable, and that, due to the chosen discretization of state space (181×181 grid), the evaluated parametrizations were sufficiently far from bifurcation lines. Since the perturbation value $\xi = 10^{-8}$ corresponds to the minimum accuracy of the fixed points, these results give confidence that stability is robustly assessed.

Furthermore, we assessed the robustness of the type of the emerging activity patterns (i.e., whether a pattern is purely spatial, purely temporal, spatiotemporal or neither) when the system is initialized farther away from the unstable fixed points. We chose five different locations in state space to represent the range of dynamical regimes in this study. Let $\tilde{u} = (\tilde{u}_e, \tilde{u}_i, \tilde{m})^\top$ be an unstable fixed point in either location in state space. We initialize

$$\tilde{u}_{\text{init}}(x) = \tilde{u} \pm (\varepsilon, \varepsilon, \varepsilon)^\top + \tilde{\xi}(x),$$

for every spatial position x on the ring, where $\tilde{\xi}(x) \in \mathbb{R}^3$ is independently drawn from a uniform distribution $\mathcal{U}(-0.01, 0.01)$ for each location. We chose the baseline value $\varepsilon \in \{0.01, 0.05, 0.1, 0.2, 0.3, 0.4\}$. We manually inspected each fixed point value $(\tilde{u}_e, \tilde{u}_i, \tilde{m})$ and adjusted the baseline accordingly: upward (i.e., $+\varepsilon$) if $(\tilde{u}_e, \tilde{u}_i, \tilde{m}) \leq (0.42, 0.42, 0.42)$, and downward (i.e., $-\varepsilon$) otherwise, so that $\tilde{u} \pm (\varepsilon, \varepsilon, \varepsilon)^\top \in [0, 1]^3$. Furthermore, we manually verified that the added noise $\tilde{\xi}(x)$ was small enough that $\tilde{u}_{\text{init}}(x) \in [0, 1]^3$ was also true everywhere.

We conducted numerical simulations for five different realizations of $\tilde{\xi}(x)$, consequently leading to 5×6 simulations per representative location in state space. This investigation showed that the variations in spatial frequencies and speed were comparably low, and that the temporal frequency remained at the same value for all simulations, independent of the initialization. For all states except the Hopf-unstable state, we observed that the resulting activity pattern was always spatiotemporal. For the Hopf-unstable state, however, a change of the baseline by $\varepsilon \geq 0.05$ led to purely temporal oscillations (see also Sec. IV).

3. Spatial and temporal frequencies

We define *one time unit* as $\text{unit}_t = 10\,000$ time-iteration steps and quantify temporal frequency by $[\frac{\text{oscillation periods}}{\text{unit}_t}]$. For brevity, we write $[\frac{\text{osc}}{\text{unit}_t}]$. This choice is based on the model's ability to generate slow oscillations (i.e., $\leq 2 \frac{\text{osc}}{\text{unit}_t}$) for finite adaptation (i.e., $b \neq 0$) as well as faster oscillations (e.g., α -like oscillations with $8\text{--}13 \frac{\text{osc}}{\text{unit}_t}$) that are generated by the excitatory-inhibitory loop [see, e.g., f_t in Fig. 10(a)]. To determine the dominant temporal frequency, we computed the power spectra $P_{sx}(f)$ of the time series of the excitatory activity for each position x . Then, we averaged over all positions,

$$\bar{P}_s(f) = \frac{1}{N} \sum_{x=1}^N P_{sx}(f),$$

and determined the frequency of maximum power of the averaged power spectrum, i.e., $f_t = \text{argmax}_f \bar{P}_s(f)$. To characterize spatial oscillations, we computed the power spectrum over space $P_{xt}(f)$ for each time step $t \in [0, T \cdot \text{unit}_t]$, where

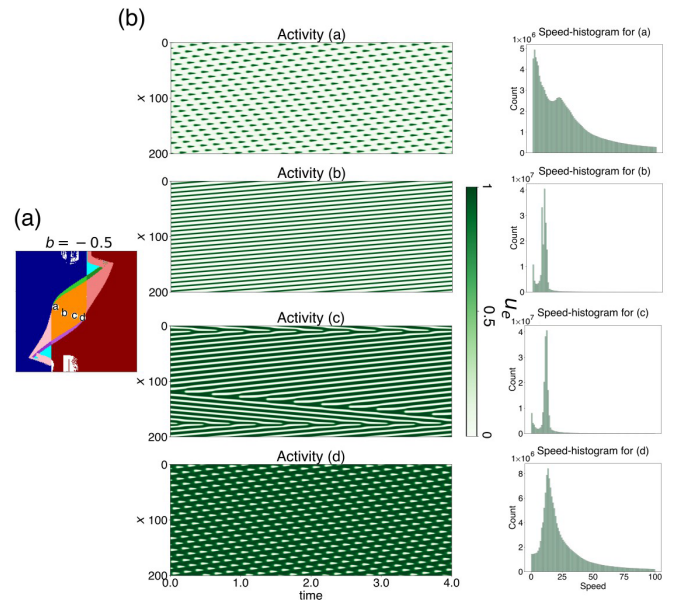


FIG. 9. Computation of dominant speed values. (a) Locations in state space for the activity patterns [panels (a)–(d)] shown in panel (b). (b) Left panels: Activity traces for $x \in [0, 200]$. Green colors denote activity values (darker green for higher, lighter green for low activity, see color bar). Right panels: Corresponding histograms of local speed values. The dominant speed corresponds to the speed value occurring most often.

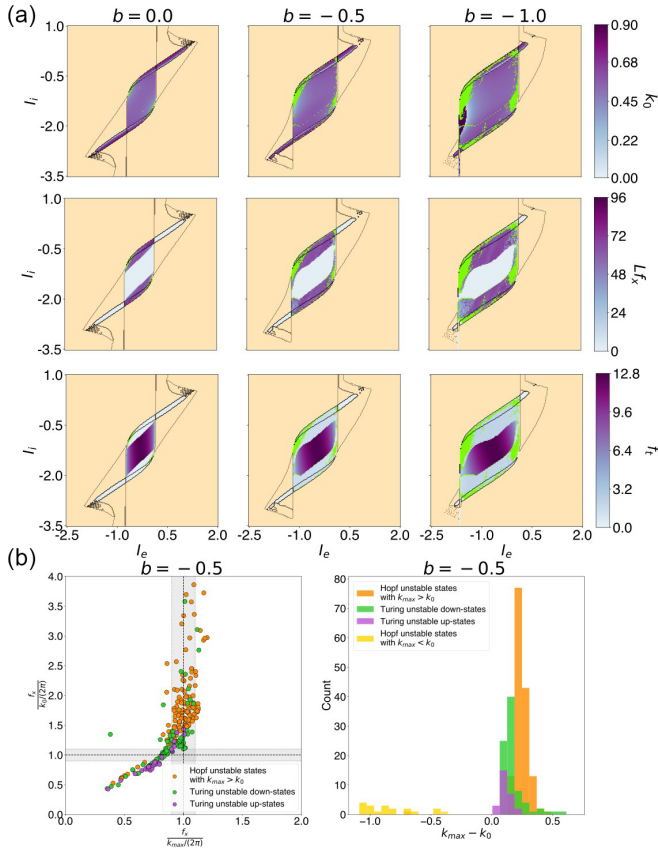


FIG. 10. Properties of the spatiotemporal patterns emerging in Hopf- and Turing-unstable states for increasing h-current strength. (a) Wave number k_0 (top row), dominant spatial frequency $L \cdot f_x$ (middle row), and dominant temporal frequency f_t (bottom row) for each location in state space. The figure shows slices of state space spanned by the external input $(I_e, I_i) \in [-2.5, 2] \times [-3.5, 1]$ for $b \in \{0, -0.5, -1.0\}$. Purple colors denote the corresponding feature values. Darker colors indicate higher values (see color bar). Yellow denotes states of no spatiotemporal activity; light green denotes states with irregular patterns with a standard deviation r of the Kuramoto-order parameter of $r > 10^{-2}$. Thin lines denote the boundaries of the dynamical regimes shown in Fig. 2(a). (b) Left: Scatter plot of the ratios between the spatial frequency f_x of the emerging patterns and the spatial frequencies corresponding to the wave numbers k_0 and $k_{\max}$ for all locations in state space from panel (a) with $b = -0.5$, which were identified as Hopf-unstable states with $k_{\max} \geq k_0$ (orange), Turing-unstable down- (purple), or Turing-unstable up-states (green). Perfect agreement with a given mode corresponds to a ratio of 1 (vertical and horizontal dashed lines). The gray regions around each ratio being 1 denote deviations smaller than 10%. Right: Distribution of the differences $k_{\max} - k_0$ for the same state space, additionally including the Hopf-unstable states with $k_{\max} < k_0$. Numerical simulations were conducted with initializations close to zero.

$T = 20$ denotes the amount of time units used after discarding the transients (see Appendix B 1). Then, we averaged over all time steps,

$$\bar{P}_x(f) = \frac{1}{T \cdot \text{unit}_t} \sum_{t=1}^{T \cdot \text{unit}_t} P_{xt}(f),$$

and determined the spatial frequency of maximum power over the averaged power spectrum, i.e., $f_x = \arg\max_f \bar{P}_x(f)$. For both temporal and spatial frequencies, activity patterns exist for which the power spectrum shows multiple peaks. In those cases, we report the temporal and spatial frequencies corresponding to the most prominent peak.

In the text, we sometimes report the value $L \cdot f_x$ instead of f_x , which correspond to the number of bumps on the ring.

4. Regularity of patterns

We characterized the spatiotemporal pattern using the Kuramoto-order parameter. We computed the analytical signal representation of the activity $u_e(x, t)$ using the Hilbert transformation:

$$z(x, t) = u_e(x, t) + i\mathcal{H}[u_e(x, t)], \quad (\text{B1})$$

where $\mathcal{H}[\cdot]$ denotes the Hilbert transformation and i the imaginary unit. Using the instantaneous phase

$$\theta(x, t) = \arctan\left(\frac{\text{Im}(z(x, t))}{\text{Re}(z(x, t))}\right), \quad (\text{B2})$$

we calculate the Kuramoto-order parameter $R(t)$ for each time step t :

$$R(t) = \left| \frac{1}{n} \sum_x e^{i\theta(x, t)} \right|,$$

and define the regularity r of a spatiotemporal pattern by its standard deviation

$$r = \sqrt{\frac{1}{T} \sum_{t=1}^T (R(t) - \bar{R})^2}, \quad \bar{R} = \frac{1}{T} \sum_{t=1}^T R(t)$$

over a time interval $[0, T]$. We considered patterns to be regular if $r \leq 10^{-2}$. This threshold corresponds to the mean over the ten most irregular patterns found when compiling Fig. 5(a).

5. Phase velocity and speed

To compute the speed in $[\frac{\text{unit}_x}{\text{unit}_t}]$, where $\text{unit}_x = \frac{1}{dx}$, of a spatiotemporal pattern, we used the approach of Ref. [85]. We first determine the analytical representation of the activity $u_e(x, t)$ as in Eq. (B1), where $\theta(x, t)$ is the instantaneous phase at position x and time step t as in Eq. (B2). The local speed $s(x, t)$ is computed from the temporal and spatial derivatives $\frac{\partial \theta}{\partial x}(x, t)$ of the instantaneous phase,

$$s(x, t) = \left| \frac{\frac{\partial \theta(x, t)}{\partial t}}{\frac{\partial \theta(x, t)}{\partial x}} \right|.$$

Since spatiotemporal patterns may be composed of traveling waves of different speeds [e.g., see Fig. 6(b), panel 5], we apply a similar approach as for the dominant spatial frequency. We compute a histogram over all local speed values appearing

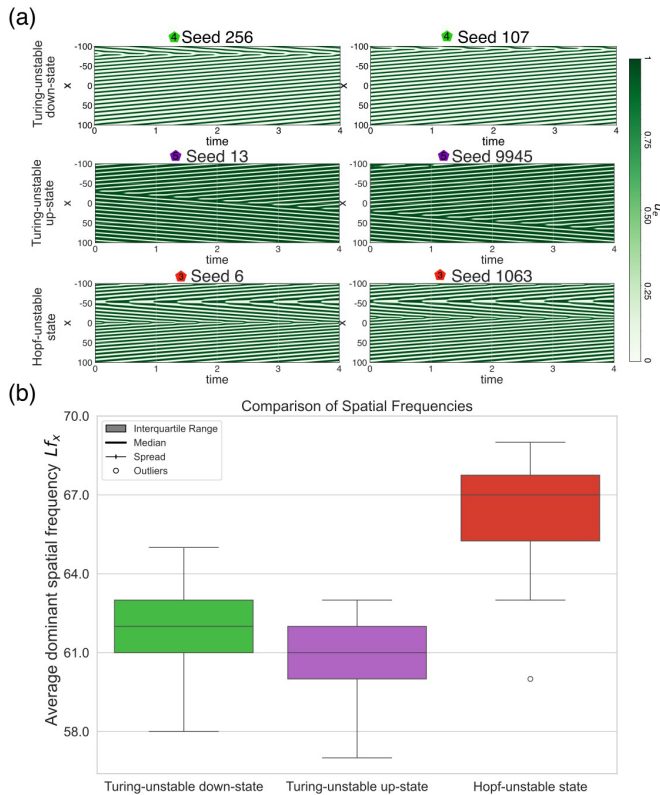


FIG. 11. (a) Activity traces 4, 6, and 3 (top to bottom row) of Fig. 2 initialized close to the fixed points of Turing instability in a down-state (first row), in an up-state (second row), and of Hopf instability but with different seeds. (b) Consistency of the spatial dynamics for 30 different seeds for each activity in panel (a). Visualized are interquartile ranges (boxes), medians (horizontal lines inside boxes), spread (error bars), and outliers outside of spread (circles) for the Turing-unstable down- (green) and up-state (purple), and the Hopf-unstable state (red).

per activity pattern and take the speed value appearing the most often. In Fig. 9, we illustrate this procedure for four different activity patterns.

6. Properties of activity patterns emerging for initializations close to zero

We conducted same analysis as for Figs. 5(a) and 5(c) but with the activity variables initialized close to zero. Figure 10(a) shows the wave number k_0 , the spatial frequency multiplied to the length of the ring, $L \cdot f_x$ (center row, effectively describing the number of bumps on the ring), and temporal frequency, f_t (bottom row), for the patterns emerging in Turing- and Hopf-unstable states for increasing adaptation strength. We see that further away from the boundaries, inside the regime of Hopf instability, purely temporal oscillations emerge with higher temporal frequencies compared to the activity patterns that emerge after initializing close to the Hopf-unstable fixed point. Closer to the boundaries, purely spatial patterns emerge for $b = 0$ that become spatiotemporal for $b \neq 0$. Figure 10(b) shows the ratio between the dominant spatial frequency f_x and the wave numbers k_0 and $k_{\max}$ for $b = -0.5$ plotted against each other (left panel) and the distribution of the differences $k_{\max} - k_0$ (right panel). As in the case of Fig. 5(c), we see that the simulated spatial frequencies predominantly correspond to $k_{\max}$ and that $k_0 > k_{\max}$, except for some locations inside the Hopf instability regime, where the simulated activity patterns were all identified as irregular.

7. Spatial frequencies of the spatiotemporal patterns emerging for different initializations

Figure 11 shows exemplary robustness of spatial dynamics of three activity traces shown in Fig. 2 and for ten different realizations of initialization. See also Appendix B 2.

- [1] M. V. Sanchez-Vives, M. Massimini, and M. Mattia, Shaping the default activity pattern of the cortical network, *Neuron* **94**, 993 (2017).
- [2] M. V. Sanchez-Vives, Origin and dynamics of cortical slow oscillations, *Curr. Opin. Physiol.* **15**, 217 (2020).
- [3] M. Steriade, A. Nunez, and F. Amzica, A novel slow (≤ 1 Hz) oscillation of neocortical neurons *in vivo*: Depolarizing and hyperpolarizing components, *J. Neurosci.* **13**, 3252 (1993).
- [4] Note, however, that cortical down-states, which correspond to so-called K complexes, have already been described in the very first sleep electroencephalography studies in the 1930s [5].
- [5] A. L. Loomis, E. N. Harvey, and G. Hobart, Further observations on the potential rhythms of the cerebral cortex during sleep, *Science* **82**, 198 (1935).
- [6] S. Brodt, M. Inostroza, N. Niethard, and J. Born, Sleep—A brain-state serving systems memory consolidation, *Neuron* **111**, 1050 (2023).
- [7] J. G. Klinzing, N. Niethard, and J. Born, Mechanisms of systems memory consolidation during sleep, *Nat. Neurosci.* **22**, 1598 (2019).
- [8] B. Rasch and J. Born, About sleep's role in memory, *Physiol. Rev.* **93**, 681 (2013).
- [9] M. Massimini, R. Huber, F. Ferrarelli, S. Hill, and G. Tononi, The sleep slow oscillation as a traveling wave, *J. Neurosci.* **24**, 6862 (2004).
- [10] E. S. L. Faber and P. Sah, Calcium-activated potassium channels: Multiple contributions to neuronal function, *Neuroscientist* **9**, 181 (2003).
- [11] G. E. Ha and E. Cheong, Spike frequency adaptation in neurons of the central nervous system, *Exp. Neurobiol.* **26**, 179 (2017).
- [12] D. A. McCormick, Neurotransmitter actions in the thalamus and cerebral cortex and their role in neuromodulation of thalamo-cortical activity, *Prog. Neurobiol.* **39**, 337 (1992).
- [13] B. E. Jones, Arousal systems, *Front. Biosci.* **8**, s438 (2003).
- [14] T.-A. E. Nghiem, N. Tort-Colet, T. Górski, U. Ferrari, S. Moghimyfiroozabad, J. S. Goldman, B. Teleńczuk, C. Capone, T. Bal, M. di Volo, and A. Destexhe, Cholinergic switch between two types of slow waves in cerebral cortex, *Cereb. Cortex* **30**, 3451 (2020).

- [15] D. Jercog, A. Roxin, P. Barthó, A. Luczak, A. Compte, and J. de la Rocha, Up-down cortical dynamics reflect state transitions in a bistable network, *eLife* **6**, e22425 (2017).
- [16] C. L. Combe and S. Gasparini, I_h from synapses to networks: HCN channel functions and modulation in neurons, *Prog. Biophys. Mol. Biol.* **166**, 119 (2021).
- [17] Y. Shu, A. Hasenstaub, and D. A. McCormick, The h-current controls cortical recurrent network activity through modulation of dendrosomatic communication, *bioRxiv* (2023).
- [18] A. Destexhe and A. Babloyantz, A model of the inward current I_h and its possible role in thalamocortical oscillations, *NeuroReport* **4**, 223 (1993).
- [19] A. Destexhe, D. A. McCormick, and T. J. Sejnowski, A model for 8–10 Hz spindling in interconnected thalamic relay and reticularis neurons, *Biophys. J.* **65**, 2473 (1993).
- [20] S. Hill and G. Tononi, Modeling sleep and wakefulness in the thalamocortical system, *J. Neurophysiol.* **93**, 1671 (2005).
- [21] S. Y. Abbas, S. W. Ying, and P. A. Goldstein, Compartmental distribution of hyperpolarization-activated cyclic-nucleotide-gated channel 2 and hyperpolarization-activated cyclic-nucleotide-gated channel 4 in thalamic reticular and thalamocortical relay neurons, *Neuroscience* **141**, 1811 (2006).
- [22] D. Mehrotra, D. Levenstein, A. J. Duszkievicz, S. S. Carrasco, S. A. Booker, A. Kwiatkowska, and A. Peyrache, Hyperpolarization-activated currents drive neuronal activation sequences in sleep, *Curr. Biol.* **34**, 3043 (2024).
- [23] L. Dalla Porta, A. Barbero-Castillo, J. Sanchez-Sanchez, N. Cancino, and M. V. Sanchez-Vives, H-current modulation of cortical up and down states, *J. Physiol.* **603**, 2409 (2025).
- [24] P. C. Bressloff, Spatiotemporal dynamics of continuum neural fields, *J. Phys. A: Math. Theor.* **45**, 033001 (2012).
- [25] B. Ermentrout, The analysis of synaptically generated traveling waves, *J. Comput. Neurosci.* **5**, 191 (1998).
- [26] G. Ermentrout and D. Terman, *Mathematical Foundations of Neuroscience, Interdisciplinary Applied Mathematics* (Springer, New York, 2010).
- [27] S. Budzinskiy, A. Beuter, and V. Volpert, Nonlinear analysis of periodic waves in a neural field model, *Chaos* **30**, 083144 (2020).
- [28] R. Erazo-Toscano and R. Osan, Synaptic propagation in neuronal networks with finite-support space-dependent coupling, *Phys. Rev. E* **107**, 034403 (2023).
- [29] O. E. Omel'chenko and C. R. Laing, Activity patterns in ring networks of quadratic integrate-and-fire neurons with synaptic and gap junction coupling, *Phys. Rev. E* **110**, 034411 (2024).
- [30] S. Coombes, Waves, bumps, and patterns in neural field theories, *Biol. Cybern.* **93**, 91 (2005).
- [31] M. R. Qubbaj and V. K. Jirsa, Neural field dynamics under variation of local and global connectivity and finite transmission speed, *Physica D* **238**, 2331 (2009).
- [32] J. D. Harris and B. Ermentrout, Traveling waves in a spatially-distributed Wilson-Cowan model of cortex: From fronts to pulses, *Physica D* **369**, 30 (2018).
- [33] J. Wyller, P. Blomquist, and G. T. Einevoll, Turing instability and pattern formation in a two-population neuronal network model, *Physica D* **225**, 75 (2007).
- [34] H. R. Wilson and J. D. Cowan, Excitatory and inhibitory interactions in localized populations of model neurons, *Biophys. J.* **12**, 1 (1972).
- [35] C. Dimulescu, R. Strömsdörfer, A. Flöel, and K. Obermayer, On the robustness of the emergent spatiotemporal dynamics in biophysically realistic and phenomenological whole-brain models at multiple network resolutions, *Front. Network Physiol.* **5**, 1589566 (2025).
- [36] D. Levenstein, G. Buzsáki, and J. Rinzel, NREM sleep in the rodent neocortex and hippocampus reflects excitable dynamics, *Nat. Commun.* **10**, 2478 (2019).
- [37] M. Torao-Angosto, A. Manasanch, M. Mattia, and M. V. Sanchez-Vives, Up and down states during slow oscillations in slow-wave sleep and different levels of anesthesia, *Front. Syst. Neurosci.* **15**, 609645 (2021).
- [38] P. C. Bressloff, Metastable states and quasicycles in a stochastic Wilson-Cowan model of neuronal population dynamics, *Phys. Rev. E* **82**, 051903 (2010).
- [39] T. Trabocchi, R. Burioni, L. de Arcangelis, and D. Fanelli, Generalized Wilson-Cowan model with short term synaptic plasticity, *Chaos, Solitons Fract.* **208**, 118286 (2026).
- [40] R. Marino, L. Buffoni, L. Chicchi, F. D. Patti, D. Febbe, L. Giambagli, and D. Fanelli, Learning in Wilson-Cowan model for metapopulation, *Neural Comput.* **37**, 701 (2025).
- [41] H. R. Wilson and J. D. Cowan, A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue, *Kybernetik* **13**, 55 (1973).
- [42] D. J. Pinto and G. B. Ermentrout, Spatially structured activity in synaptically coupled neuronal networks: I. Traveling fronts and pulses, *SIAM J. Appl. Math.* **62**, 206 (2001).
- [43] S. Amari, Dynamics of pattern formation in lateral-inhibition type neural fields, *Biol. Cybern.* **27**, 77 (1977).
- [44] S. E. Folias and P. C. Bressloff, Breathing pulses in an excitatory neural network, *SIAM J. Appl. Dyn. Syst.* **3**, 378 (2004).
- [45] Z. P. Kilpatrick and P. C. Bressloff, Effects of synaptic depression and adaptation on spatiotemporal dynamics of an excitatory neuronal network, *Physica D* **239**, 547 (2010).
- [46] R. Curtu and B. Ermentrout, Pattern formation in a network of excitatory and inhibitory cells with adaptation, *SIAM J. Appl. Dyn. Syst.* **3**, 191 (2004).
- [47] M. Augustin, J. Ladenbauer, and K. Obermayer, How adaptation shapes spike rate oscillations in recurrent neuronal networks, *Front. Comput. Neurosci.* **7**, 76 (2013).
- [48] C. Cakan and K. Obermayer, Biophysically grounded mean-field models of neural populations under electrical stimulation, *PLoS Comput. Biol.* **16**, e1007822 (2020).
- [49] C. Cakan, C. Dimulescu, L. Khakimova, D. Obst, A. Flöel, and K. Obermayer, Spatiotemporal patterns of adaptation-induced slow oscillations in a whole-brain model of slow-wave sleep, *Front. Comput. Neurosci.* **15**, 800101 (2022).
- [50] J. Ladenbauer, M. Augustin, and K. Obermayer, How adaptation currents change threshold, gain, and variability of neuronal spiking, *J. Neurophysiol.* **111**, 939 (2014).
- [51] M. Mattia and M. V. Sanchez-Vives, Exploring the spectrum of dynamical regimes and timescales in spontaneous cortical activity, *Cognit. Neurodyn.* **6**, 239 (2012).
- [52] F. C. Roth and H. Hu, An axon-specific expression of HCN channels catalyzes fast action potential signaling in GABAergic interneurons, *Nat. Commun.* **11**, 2248 (2020).
- [53] HCN channels form the biophysical substrate of h-current-based adaptation.

- [54] S. Rich, T. A. Valiante, and J. Lefebvre, H- and m-channel overexpression promotes seizure-like events by impairing the ability of inhibitory neurons to process correlated inputs, *PLoS Comput. Biol.* **21**, e1013199 (2025).
- [55] M. D'Andola, B. Rebollo, A. G. Casali, J. F. Weinert, A. Pigorini, R. Villa, M. Massimini, and M. V. Sanchez-Vives, Bistability, causality, and complexity in cortical networks: An *in vitro* perturbational study, *Cereb. Cortex* **28**, 2233 (2018).
- [56] M. Dasilva, A. Camassa, A. Navarro-Guzman, A. Pazienti, L. Perez-Mendez, G. Zamora-López, M. Mattia, and M. V. Sanchez-Vives, Modulation of cortical slow oscillations and complexity across anesthesia levels, *NeuroImage* **224**, 117415 (2021).
- [57] M. V. Sanchez-Vives and D. A. McCormick, Cellular and network mechanisms of rhythmic recurrent activity in neocortex, *Nat. Neurosci.* **3**, 1027 (2000).
- [58] Z. P. Kilpatrick, Wilson-Cowan model, in *Encyclopedia of Computational Neuroscience*, edited by D. Jaeger and R. Jung (Springer, New York, NY, 2013), pp. 1–5.
- [59] L. Papadopoulos, C. W. Lynn, D. Battaglia, and D. S. Bassett, Relations between large-scale brain connectivity and effects of regional stimulation depend on collective dynamical state, *PLoS Comput. Biol.* **16**, e1008144 (2020).
- [60] T. Friedlander and N. Brenner, Adaptive response by state-dependent inactivation, *Proc. Natl. Acad. Sci. USA* **106**, 22558 (2009).
- [61] I. Timofeev, M. Bazhenov, T. Sejnowski, and M. Steriade, Cortical hyperpolarization-activated depolarizing current takes part in the generation of focal paroxysmal activities, *Proc. Natl. Acad. Sci. USA* **99**, 9533 (2002).
- [62] H.-Y. Chu and X. Zhen, Hyperpolarization-activated, cyclic nucleotide-gated (HCN) channels in the regulation of midbrain dopamine systems, *Acta Pharmacol. Sin.* **31**, 1036 (2010).
- [63] C. Ganguly, S. S. Bezugam, E. Abs, M. Payvand, S. Dey, and M. Suri, Spike frequency adaptation: Bridging neural models and neuromorphic applications, *Commun. Eng.* **3**, 22 (2024).
- [64] D. A. McCormick and H. C. Pape, Properties of a hyperpolarization-activated cation current and its role in rhythmic oscillation in thalamic relay neurones, *J. Physiol.* **431**, 291 (1990).
- [65] Reference [33], however, assumes that the fixed point values $\tilde{u}_e$ and $\tilde{u}_i$ are equal.
- [66] Reference [32] investigates the stability of homogeneous equilibria for the two-population model (i.e., $b = 0$).
- [67] Á. Byrne, D. Avitabile, and S. Coombes, Next-generation neural field model: The evolution of synchrony within patterns and waves, *Phys. Rev. E* **99**, 012313 (2019).
- [68] H. G. E. Meijer and S. Coombes, Travelling waves in a neural field model with refractoriness, *J. Math. Biol.* **68**, 1249 (2014).
- [69] States marked in yellow in the regions of Turing-unstable up- and down-states in bi are shown in Figs. 5(d) and 6(e) may also support regular spatiotemporal patterns if another initialization would have been chosen.
- [70] L. M. Giocomo and M. E. Hasselmo, Time constants of h current in layer II stellate cells differ along the dorsal to ventral axis of medial entorhinal cortex, *J. Neurosci.* **28**, 9414 (2008).
- [71] A. Bhattacharjee and L. K. Kaczmarek, For K^+ channels, Na^+ is the new Ca^{2+} , *Trends Neurosci.* **28**, 422 (2005).
- [72] D. A. Brown and P. R. Adams, Muscarinic suppression of a novel voltage-sensitive K^+ current in a vertebrate neurone, *Nature (London)* **283**, 673 (1980).
- [73] P. C. Schwindt, W. J. Spain, and W. E. Crill, Long-lasting reduction of excitability by a sodium-dependent potassium current in cat neocortical neurons, *J. Neurophysiol.* **61**, 233 (1989).
- [74] D. A. Brown and W. H. Griffith, Calcium-activated outward current in voltage-clamped hippocampal neurones of the guinea-pig, *J. Physiol.* **337**, 287 (1983).
- [75] C. M. Upchurch, C. L. Combe, C. J. Knowlton, V. G. Rousseau, S. Gasparini, and C. C. Canavier, Long-term inactivation of sodium channels as a mechanism of adaptation in CA1 pyramidal neurons, *J. Neurosci.* **42**, 3768 (2022).
- [76] C.-H. Lee and R. MacKinnon, Structures of the human HCN1 hyperpolarization-activated channel, *Cell* **168**, 111 (2017).
- [77] A. Mironenko, U. Zachariae, B. L. de Groot, and W. Kopec, The persistent question of potassium channel permeation mechanisms, *J. Mol. Biol.* **433**, 167002 (2021).
- [78] H.-C. Pape, Queer current and pacemaker: The hyperpolarization-activated cation current in neurons, *Annu. Rev. Physiol.* **58**, 299 (1996).
- [79] M. Biel, C. Wahl-Schott, S. Michalakakis, and X. Zong, Hyperpolarization-activated cation channels: From genes to function, *Physiol. Rev.* **89**, 847 (2009).
- [80] R. C. Budzinski, T. T. Nguyen, G. B. Benigno, J. Doãn, J. Mináč, T. J. Sejnowski, and L. E. Muller, Analytical prediction of specific spatiotemporal patterns in nonlinear oscillator networks with distance-dependent time delays, *Phys. Rev. Res.* **5**, 013159 (2023).
- [81] J. A. Roberts, L. L. Gollo, R. G. Abeysuriya, G. Roberts, P. B. Mitchell, M. W. Woolrich, and M. Breakspear, Metastable brain waves, *Nat. Commun.* **10**, 1056 (2019).
- [82] M. Martin and M. G. Pedersen, Modelling and analysis of cAMP-induced mixed-mode oscillations in cortical neurons: Critical roles of HCN and M-type potassium channels, *PLoS Comput. Biol.* **20**, e1011559 (2024).
- [83] <https://github.com/ronja-roevardotter/equivalent-adaptation-wilson-cowan-field.git>.
- [84] R. Strömsdörfer, Framework for reproducibility, version 1.1, Zenodo (2026), <https://zenodo.org/records/19455050>.
- [85] D. Rubino, K. A. Robbins, and N. G. Hatsopoulos, Propagating waves mediate information transfer in the motor cortex, *Nat. Neurosci.* **9**, 1549 (2006).