Reaction-diffusion-like formalism for plastic neural networks reveals dissipative solitons at criticality

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Self-organized structures in networks with spike-timing dependent synaptic plasticity (STDP) are likely to play a central role for information processing in the brain. In the present study we derive a reaction-diffusion-like formalism for plastic feed-forward networks of nonlinear rate-based model neurons with a correlation sensitive learning rule inspired by and being qualitatively similar to STDP. After obtaining equations that describe the change of the spatial shape of the signal from layer to layer, we derive a criterion for the nonlinearity necessary to obtain stable dynamics for arbitrary input. We classify the possible scenarios of signal evolution and find that close to the transition to the unstable regime metastable solutions appear. The form of these dissipative solitons is determined analytically and the evolution and interaction of several such coexistent objects is investigated.

I. INTRODUCTION

Activity in neuronal networks influences their coupling structure due to spike time-dependent synaptic plasticity (STDP) [1], which, in turn, influences the activity. Several works analytically investigated structures appearing in networks of neurons with plastic synapses under the influence of external signals. These studies required special network architectures, investigating, e.g., a kind of possible "elementary cell" of the network [2]. Other works considered all-to-all connected networks [3] or averages over realizations of the activity in space [4] or systems without continuous spatial dimension [5]. Hebbian [6] and similar learning rules, which can be considered as a simple STDP-like rule, are used in many neural network models, like Hopfield and Boltzmann networks [7]. These works employ the energy minimization principle known in physics and set the values of synaptic weights according to the patterns to be stored, without considering the time evolution of the weights explicitly. These systems are able to store one level associations between patterns and recognize and restore externally applied and previously learned patterns. The memory capacity as well as the time required to recognize an input have been investigated [7]. Activity propagation in non-plastic feed-forward systems was considered in [8]. A set of integro-differential equations, describing a spatially extended network, was introduced in [9] as the neural field model. A scheme of solution for a simplified version neglecting refractoriness [10] was later extended for neurons with adaptation [11] and different nonlinearities [12]. The spatial and structural organization of the cortex [13,14] separates different neural inputs either in real space or in an effective space that represents a continuum of features. For example, the orientation selectivity of neurons in the visual cortex is represented in some species by neurons topologically arranged on a one-dimensional ring [15]. One suggested mechanism [16,17] to implement short-term memory is by localized bump solutions, which are also considered in [12]. The latter work shows the relation between the formalism of reaction-diffusion-like systems and spatially extended non-plastic neural networks.

Our work demonstrates such a relation for neural networks with long-term plasticity. The formalism thus fills the gap between a series of studies of plastic networks without spatial dimension and the formalism describing activity in spatially extended networks. The presented analysis therefore opens the possibility to study the transfer of short-term memory, encoded by bump solutions, into long-term memory, stored by synaptic modifications. Here we analytically consider a feed-forward network with space-dependent connectivity and linear-nonlinear model neurons with a simple STDP-inspired synaptic learning rule, similar to the BCM rule [18]. We reduce the discrete problem by the diffusion approximation to obtain an equation similar, but not equivalent, to a reaction-diffusion equation with one component, also called the Kolmogorov-Petrovsky-Piskounov equation [19,20]. We derive the requirements on the nonlinearity necessary for a regime of stable signal propagation, exposing that fine-tuning of parameters is necessary, explaining earlier results [21]. The bump solutions that are stable in the critical and metastable in the subcritical regime are described analytically. The interneural connections inside a bump are strengthened, resembling cell assemblies [22] and showing how externally presented objects (external input) change intrinsic system properties (connectivity).

We further investigate how several such coexisting bump solutions mutually influence each other. In particular, we study how their interaction depends on the spatial extent of the bumps, the distance between them, and the system parameters. In the regime close to stable propagation from one layer to the next we find that several coexisting activity bumps can either unite or remain disjointed, depending on the initial conditions. Their unification can be interpreted as an emergence of connections between cell-assemblies. In this way the system is able to represent a set of associations between internal representations of corresponding external stimuli. The improved formalism can be generalized to neural networks with several neuron types.

In the presented analysis we focus on the stationary state into which the network settles after a long waiting time. In

this regard, time is not explicitly represented. Still, one can relate the change of the activity distribution from one layer to the next to the evolution of activity in time in a single recurrently connected layer, where the layers play the role of time slices. As shown in the discussion, such a mapping is strictly valid for non-plastic networks. Moreover, for the most interesting case of metastable solutions, the presented results for plastic feed-forward networks can serve as approximations to the solutions expected in recurrent plastic networks evolving in time.

II. RESULTS

A. Model definition

Here we consider feed-forward networks consisting of M layers of N neurons each. A neuron at position $\tilde{x}$ in layer $n+1$ gets as input $u_{\tilde{x}}$ the weighted sum of outputs r of an odd number K of neurons from the neighborhood in the previous layer n, $u_{\tilde{x}} = \sum_{x=\tilde{x}-(K-1)/2}^{x=\tilde{x}+(K-1)/2} w_{\tilde{x}x} r_x$, where the indices $\tilde{x}$ and x describe the positions of the postsynaptic neuron in the layer $n+1$, and of the presynaptic neuron in the layer n, respectively. Here $w_{\tilde{x}x}$ is the synaptic weight from neuron x to neuron $\tilde{x}$. The neuron's output $r = f(u)$ is given by its input u mapped by the nonlinear function f. The function f reflects the nonlinear nature of neurons. Some neuron models explicitly contain a nonlinear component that continuously maps their input to their output, in other models the nonlinearity results from a threshold on the membrane voltage which needs to be reached to let the neuron emit spike. The nonlinearity also captures the saturation of the outgoing activity due to the limitation of the cell's resources, often modeled by the saturating part of the ubiquitously found sigmoidal-shaped nonlinearities. For simulations we used $f(x) = A/(1 + e^{-\beta(x-\theta)}) - A/(1 + e^{\beta\theta})$. The network architecture is illustrated in Fig. 1. The absence of feedback allows the solution of the system, finding successively the activities and synaptic weights for each pair of layers using the solution for the activity distribution of the previous layer as an input.

We assume a Hebbian plasticity rule

$$\dot{w}_{\tilde{x}x} = -\alpha(w_{\tilde{x}x} - w_0) + \gamma r_x r_{\tilde{x}} \qquad (1)$$

for the presynaptic neuron x and the postsynaptic neuron $\tilde{x}$. If a stationary solution exists it can be found requiring $\dot{w}_{\tilde{x}x} = 0$
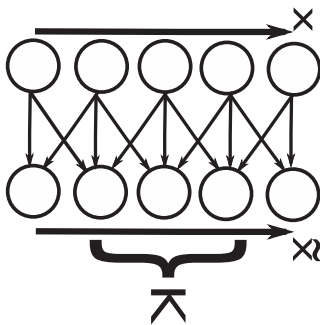

FIG. 1. Two adjacent layers in the considered feed-forward architecture. Synapses between layers obey the plasticity rule (1).

as

$$w_{\tilde{x}x} = w_0 + \frac{\gamma}{\alpha} r_x r_{\tilde{x}} = w_0 + \frac{\gamma}{\alpha} f(u_x) f(u_{\tilde{x}}). \qquad (2)$$

In the following we use $\xi_x = u_{\tilde{x}}$ as the summed input to the postsynaptic neuron to better distinguish it from the presynaptic neuron's u.

In equilibrium, after the learning processes stopped, ξ is found as a solution of the self-consistency equation

$$\xi_x = \check{f}(r_x^{\xi}) = \sum_{\Delta x = -(K-1)/2}^{(K-1)/2} w_{x\,x+\Delta x}\, r_{x+\Delta x}$$

$$\stackrel{(2)}{=} w_0 \sum_{\Delta x = -(K-1)/2}^{(K-1)/2} r_{x+\Delta x} + \frac{\gamma}{\alpha} r_x^{\xi} \sum_{\Delta x = -(K-1)/2}^{(K-1)/2} r_{x+\Delta x}^2 \qquad (3)$$

with $r^{\xi} = f(\xi)$ and the symbol $\check{}$ denoting the inverse function.

In the approximation neglecting further derivatives (that is exact for $K=3$) one can replace the sums over the neighborhood appearing in Eq. (3) with $(K + a\partial_x^2)$, where $a = \sum_{n=0}^{(K-1)/2} n^2 = (K-1)K(K+1)/24$ and ∂_x denotes the discrete lattice derivative. Subsequently, we make the transition from a discrete index x to a continuous variable, also denoted as x, where ∂_x becomes the ordinary derivative. So, the activity in the system arises from the interplay between the diffusion described by the ∂_x^2-operator and two types of nonlinearities: The explicit nonlinearity is given by the activation function f of the neuron, the implicit nonlinearity results from the term r_x^2 in Eq. (3), originating in the (Hebbian) plasticity rule. In this approximation, Eq. (3) can be rewritten as

$$\xi = \check{f}(r^{\xi}) = w_0(K + a\partial_x^2)r + \frac{\gamma}{\alpha} r^{\xi}(K + a\partial_x^2)r^2. \qquad (4)$$

B. Analysis of global stability and self-reproducing solutions

One can search for possible stable solutions $\xi_x = u_x$, satisfying

$$\check{f}(r) = w_0(K + a\partial_x^2)r + \frac{\gamma}{\alpha} r(K + a\partial_x^2)r^2, \qquad (5)$$

where $r_x = f(u_x)$. There are no terms explicitly depending on the variable x, so one can reduce the order of the equation by introducing $y(r) = [\partial_x r](r)$, the derivative of r depending on r. We can hence express the second derivatives in Eq. (5) as

$$\partial_x^2 r = \partial_x y = \partial_r y\, \partial_x r = y\, \partial_r y,$$

$$\partial_x^2(r^2) = 2(\partial_x r)^2 + 2r\, \partial_x^2 r = 2y^2 + 2ry\, \partial_r y = 2z + r\, \partial_r z,$$

$$(6)$$

where we used the substitution $z(r) = y^2 = (\partial_x r)^2$ in the last step. Equation (5) then takes the form of a linear differential equation in z:

$$\check{f}(r) = w_0(K r + a y\, \partial_r y) + \frac{\gamma}{\alpha}(r^3 K + ar(2z + r\, \partial_r z))$$

$$= w_0 K r + \frac{\gamma}{\alpha} r^3 K + 2\frac{\gamma}{\alpha} ar\, z + \left(\frac{1}{2} w_0 a + \frac{\gamma}{\alpha} ar^2\right) \partial_r z,$$

$$(7)$$

replacing $y\,\partial_r y$ in the first line with $\frac{1}{2}\partial_r z$ in the second line. The solution of the corresponding homogeneous equation $2\frac{\gamma}{\alpha}arz + (\frac{1}{2}w_0 a + \frac{\gamma}{\alpha}ar^2)\,\partial_r z = 0$ is $H(r) = c\frac{2}{a(w_0+2\frac{\gamma}{\alpha}r^2)}$ (with an arbitrary constant c), and as solution of Eq. (7) one gets

$$z(r) = \frac{2}{a\big(w_0 + 2\frac{\gamma}{\alpha}r^2\big)} \int^r \underbrace{\big(\check{f}(r') - K\big(w_0 + \frac{\gamma}{\alpha}r'^2\big)r'\big)}_{\equiv q(r')} dr',$$

(8)

where we used that the factor in front of $\partial_r z$ cancels with H^{-1}.

We are seeking solutions that start at $r = 0$. As z is the square of a real number and hence cannot be negative, a solution that exists for all r has to satisfy $Q(r) = \int_0^r q(r')\,dr' \geqslant 0$. We call $r_{\max}$ the largest value of r reached, for which $\partial_x r = 0$ and therefore $z(r_{\max}) = 0$, from which follows

$$Q(r_{\max}) = 0.$$

(9)

For this case $Q(r)$, $q(r)$ and the stable solution $r(x)$ are shown in Fig. 2. The physical meaning of $q(r)$ is the competition between the nonlinearity f and the effective nonlinearity $K(w_0 + \frac{\gamma}{\alpha}r^2)r$ that describe the propagation of r neglecting diffusion: $K(w_0 + \frac{\gamma}{\alpha}r^2)r$ is the value of a postsynaptic neuron's membrane potential ξ for the case that presynaptic and postsynaptic neurons have $u = \check{f}(r)$. So, a positive $q(r)$ indicates a decrease of u and r from one layer to the next, negative $q(r)$ corresponds to both measures increasing. So, in a stable system we must have $Q(r) \geqslant 0$ for all $r \geqslant 0$. By definition, $Q(r = 0) = 0$. If there are no other r at which $Q(r) = 0$, no self-consistent solution exists that propagates from layer to layer without change. If one tries to construct the stable solution according to Eq. (8) for this case, one will always have positive $\partial_x r$ for every $r > 0$, which means that for every $r > 0$ "external support" (additional input) is needed to

compensate the diffusion effects. Without such support, every finite signal will decay after some layers. If, in contrast, a position $r > 0$ exists at which $Q(r) = 0$, a solution exists that has this r as the maximum. If $q(r) = \partial_r Q(r)$ at that point is negative, an arbitrary small positive perturbation added to this maximum r will grow. So, $Q(r) < 0$ for some r means the absence of a stable solution and explosion of activity for sufficiently strong activation patterns.

The solution is given in the form $z(r) = (\partial_x r)^2$, where the choice of a positive or negative sign in taking the square root corresponds to a solution that is first increasing or decreasing, respectively, when moving from left to right. The length of a "plateau" with $\partial_x r = 0$ and $Q(r_{\max}) = 0$ is an arbitrary parameter of the solution which can be chosen freely.

The form of the remainder of the bump—the left and right wings $r = p(x)$—is independent of the plateau's width and can be obtained analytically from Eq. (8) or by numerical integration as the inverse function of

$$\check{p}(r) = \int^r \pm 1/\sqrt{z}\,dr = \int^r \pm 1 \Big/ \sqrt{\frac{2}{a\big(w_0 + 2\frac{\gamma}{\alpha}r^2\big)}Q(r)}\,dr,$$

(10)

integrating from an arbitrary value of r between 0 and $r_{\max}$ and taking plus to indicate the left and minus to indicate the right wing.

C. Long-living solutions in the sub-critical regime

If no $r_{\max} > 0$ with $Q(r_{\max}) = 0$ exists, but $Q(\tilde{r}_{\max})$ has a local minimum close to zero, one gets similar structures as the "immortal" solutions for Eq. (9). The bump solutions propagate over large but finite numbers of layers before they disappear. This number is approximately proportional to the initial width S of the plateau: for S larger than K, the successive reduction of this width does not affect the processes on the borders, and the rate of reduction s of the plateau's width from layer to layer, is approximately constant, depending only on network parameters as shown in Fig. 3. The value of s can be calculated as the propagation speed that makes the solution stable. Obtaining the rate profile for the previous layer as a slightly shifted version $r(x) - s\partial_x r(x)$ of the profile $r(x)$ in the current layer, one obtains from Eq. (4)

$$\check{f}(r) = w_0\big(K + a\partial_x^2\big)(r - s\partial_x r) + \frac{\gamma}{\alpha}r\big(K + a\partial_x^2\big)(r - s\partial_x r)^2$$
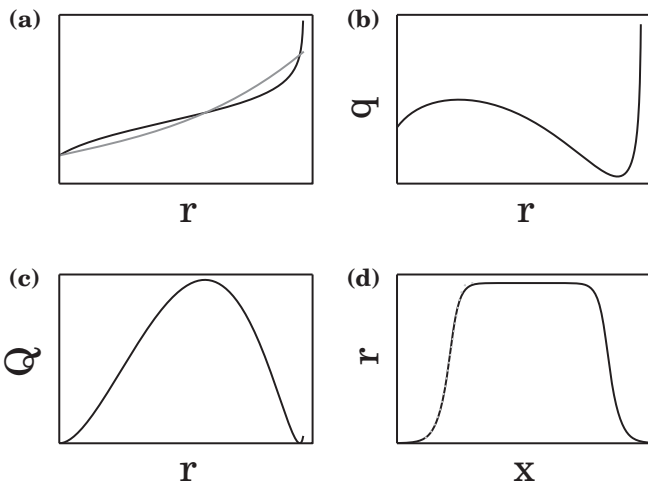

FIG. 2. Stable solution in the critical regime. (a) Explicit $\check{f}(r)$ (black) and implicit $K(w_0 + \frac{\gamma}{\alpha}r^2)r$ nonlinearity (gray). (b) Their difference, $q(r)$. (c) $Q(r) = \int q(r)dr$, a minimum of Q of 0 enables a stable non-trivial solution $r(x)$ shown in (d)—theoretical prediction of the stable solution with dashed line and simulation results with solid line. Simulation parameters: $N = 800$, $M = 400$, $K = 41$, $w_0 = 0.99/K$, $\gamma = 0.99/K$, $\theta = 0.6$, $\beta = 3.6$, $A = 1.0754$.
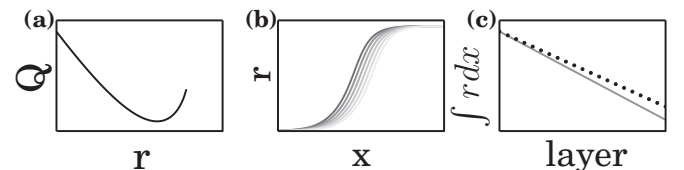

FIG. 3. Single bump evolution in subcritical regime. (a) $Q(r)$ near its minimum close to but bigger than 0. (b) Rate profiles $r(x)$ in different layers showing the reduction of the plateau's width for a long-living rate profile leading to linear decrease with the layer's number of $\int r(x)\,dx$. (c) The theoretical expectation (12) and the simulated result for $\int r(x)\,dx$. Parameters as for Fig. 2 apart from $A = 1.0745$.

or, after sorting, neglecting terms $O(s^2)$, using the definition of $q(r)$ in Eq. (8) and multiplying with $\partial_x r$

$$q(r)\partial_x r - sw_0 K(\partial_x r)^2 - sw_0 a\partial_x^3 r\,\partial_x r + aw_0\partial_x^2 r\,\partial_x r$$
$$= -2s\frac{\gamma}{\alpha}Kr^2(\partial_x r)^2 + \frac{\gamma}{\alpha}ar\partial_x r\partial_x^2(r^2) - 2s\frac{\gamma}{\alpha}ar\partial_x^2(r\partial_x r)\partial_x r$$

which, after integrating over x from minus infinity to the beginning of the plateau, leads to

$$Q(\tilde{r}_{\max}) = -s\int_0^{\tilde{r}_{\max}} w_0 K\partial_x r + aw_0\partial_x^3 r + \frac{\gamma}{\alpha}\big(2Kr^2\partial_x r$$
$$+ 2ar\partial_x^2(r\partial_x r) + ar\partial_x^2(r^2)\big) + aw_0\partial_x^2 r\,dr. \quad (11)$$

The last two terms in the latter expression vanish, because $\int_0^{\tilde{r}_{\max}}\partial_x^2 r\ dr = \int_0^{\tilde{r}_{\max}} y\partial_r y\ dr = \frac{1}{2}(\partial_x r)^2|_{r=0}^{r=\tilde{r}_{\max}} = 0$. Further we have $\int_0^{\tilde{r}_{\max}} r\partial_x^2(r^2)\ dr = \frac{1}{2}\int_0^{\tilde{r}_{\max}}\partial_x^2(r^2)\ dr^2 = \frac{1}{2}\int_0^{\tilde{r}_{\max}^2} y_2\partial_{r^2}y_2\ dr^2 = \frac{1}{4}(\partial_x(r^2))^2|_{r=0}^{r=\tilde{r}_{\max}} = 0$ with $y_2 = [\partial_x(r^2)]$ (r^2) analog to $y(r) = [\partial_x r](r)$, because $\tilde{r}_{\max}$ is the plateau height and derivatives of r-dependent functions are 0. One can therefore obtain s with

$$s = -Q(\tilde{r}_{\max})\Big/\Big(\int_0^{\tilde{r}_{\max}}\big(w_0 K\partial_x r + 2\frac{\gamma}{\alpha}Kr^2\partial_x r$$
$$+ 2\frac{\gamma}{\alpha}ar\partial_x^2(r\partial_x r) + aw_0\partial_x^3 r\big)\,dr\Big). \quad (12)$$

We can replace $\partial_x r$ with the dependence $\partial_x r = \sqrt{z(r)}$ given by Eq. (8) obtained for $Q(\tilde{r}_{\max}) = 0$. This approximation is meaningful for integrative quantities that are not influenced strongly by the local variation of Q near $\tilde{r}_{\max}$. The chain rule allows the replacement of ∂_x with $\partial_x r\partial_r$, in this way one can express s in terms of the integral of the function containing $z(r)$ over r.

To understand how the system represents two or more coexistent signals, we investigate the situation with two coexistent metastable solutions. Two such bumps can unite into one if the minimal amplitude of r between their borders becomes big enough for self-generated growth before one of the plateaus disappears.

Without loss of generality we take $x = 0$ for the midpoint between the bumps. If the distance between the two closer ends of the bumps' plateaus is larger than some critical value, the minimal $r = r_{\min}$ at the position $x = 0$ decays. One can roughly estimate the change $\delta r_{\min}$ of $r_{\min}$ from one layer to the next, approximating $r(x)$ near $x = 0$ with the direct sum of the two bumps' wings, i.e., $r = p(x + \check{p}(r_{\min}/2)) + p(-x + \check{p}(r_{\min}/2))$ with $p(x)$ denoting a wing of a bump with $p(0) = \tilde{r}_{\max}$ at the plateau's edge. The factor $1/2$ appears because the direct sum of two identical bump solutions approximately produce the value $r_{\min}$. In this approximation

$$\delta r_{\min}(r_{\min}) = r_{\min}^{\text{new}}(r_{\min}) - r_{\min},$$
$$r_{\min}^{\text{new}} = f\big(\big[w_0\big(K + a\partial_x^2\big)r + r\big(K + a\partial_x^2\big)r^2\big]\big|_{x=0}\big) \quad (13)$$

The rate of change at the minimum $\delta r_{\min}(r_{\min})$ is shown in Fig. 4. The critical distance is given by $\check{p}(r_{\min}^{\text{crit}}/2)$, $\delta r_{\min}$ $(r_{\min}^{\text{crit}}) = 0$. For larger distances no direct unification of two bumps is possible independent of their plateaus' widths.
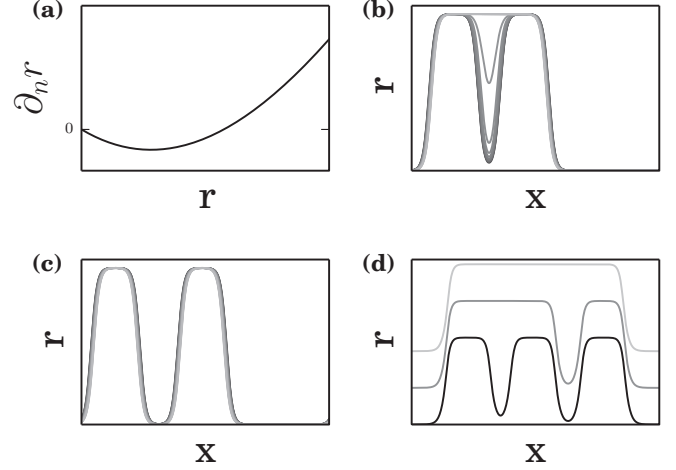

FIG. 4. Coexisting bumps in sucritical regime. (a) Theoretical prediction of the change of minimal activity $r_{\min}$ between bumps after one layer. (b) Propagation of two bumps uniting to one. (c) Two bumps remain disjointed, because their initial distance exceeds the maximal distance for unification. (d) Rate profiles in three layers. The activity of the bumps is shifted upwards in proportion to the layer number for clearer visual display. The evolution over layers illustrates the construction of an "association tree": first the left and the middle bumps are joint, and later the right one. Parameters as for Fig. 3 apart from $\gamma = 0$, $w_0 = 1.4/K$, $\beta = 3.63$ for (a)–(c).

The "next generation" of bumps resulting from the merging of two bumps of the previous generation can interact in the same way with each other as well as with the bumps of previous generations that are still alive. In this way, an association tree reflecting the input structure can be created, as illustrated in Fig. 4.

III. DISCUSSION

We obtain equations describing the propagation of activity from layer to layer in feed-forward networks of nonlinear rate neurons with an STDP-inspired plasticity rule. We find that the stability of the considered network is determined by the sign of the minimum of the function $Q(r)$: for positive sign, every perturbation decays, for negative sign activity explodes for any sufficiently strong perturbation. If the minimum is 0, stable attractive solutions exist. They have an analytically obtained form containing a plateau of variable width. So, precise tuning of parameters is required to get stable propagation of activity patterns unchanged from layer to layer, in agreement with earlier simulation results of [21]. A sigmoidal form of the nonlinearity f can help to get an alteration of the signs of $q = \partial_r Q(r)$, necessary to ensure the existence of a minimum of $Q(r) = 0$ at a non-vanishing activity level $r > 0$. A sigmoidal f is therefore a natural choice to bring the system close to criticality. The qualitative form of the gain function found here is in line with the sigmoidal form derived in [23] for feed-forward classification networks. The argumentation and the network model of this earlier work are, however, quite different. Their model does not include spatial organization. Rather, the authors find the sigmoid resulting from the requirement of optimal stability in the recognition of presented and previously learned patterns, without investigating the learning process itself. For the latter they employ the known error backpropagation mechanism,

fixing the synaptic weights prior to the consideration of the neuronal activation dynamics. Employing field theoretic arguments, the sigmoid is found as a soliton (kink) solution, where the input strength to the nonlinearity plays the role of space. The dissipative soliton solutions in our work, in contrast, are solutions in real space. Similar long-living bump solutions exist in systems with positive minima of $Q(r)$ close to 0. These solutions decay with a velocity increasing with the value of this minimum. Two bumps can unite if the interplay of the diffusion and the nonlinearity between them overcomes the decay when propagating from one layer to the next; otherwise they remain disjointed. For a united bump the same scenarios exist, so a kind of association tree can appear in this way.

Qualitatively, the central results presented in this article do not require the existence of the correlation sensitive term ($\gamma \neq 0$) and exist also in systems with static synapses, for which the correspondence to differential equations is known [12]. For $\gamma = 0$ Eq. (5) is rewritten as $q(r) = aw_0 \partial_x^2 r$, describing the stable solution of a reaction-diffusion equation (RDE) for one chemical with the reaction nonlinearity q and diffusion coefficient aw_0. One can also interpret the layers in the network as different states of the system evolution in time on a discretized time grid. The corresponding time-continuous equation $\partial_t u = aw_0 \partial_x^2 r - q(r)$ with redefined $q(r) = \check{f}(r')/\tau_m - Kw_0 r$ for the presence of a linear leak $-u/\tau_m$ is analog to a RDE for the time evolution of a system with one chemical. Dissipative solitons are known to be solutions of such systems [20] and correspond to the bump solutions (8). The non-trivial result is that such solutions exist also for arbitrary learning rates $\gamma \neq 0$ and that their shape can be obtained analytically.

A more general equation

$$q(r) = \sum_i D_i(r) \partial_x^2 F_i(r) \qquad (14)$$

of the same type as Eq. (5), but with an arbitrary number of functions under the second derivative is solved with the same substitutions z, y:

$$q(r) = \sum_i D_i(r)\left((\partial_x^2 r)\partial_r F_i(r) + (\partial_x r)^2 \partial_r^2 F_i(r) \right)$$

$$= \frac{1}{2}\left(\sum_i D_i(r)\partial_r F_i(r) \right)\partial_r z + \left(\sum_i D_i(r)\partial_r^2 F_i(r) \right) z, \qquad (15)$$

providing the solution in the form

$$z(r) = 2H(r) \int H^{-1}(r') \frac{q(r')}{\sum_i D_i(r')\partial_{r'} F_i(r')}\, dr',$$

$$H(r) = \exp\left(-2\int^r \frac{\sum_i D_i(r')\partial_{r'}^2 F_i(r')}{\sum_i D_i(r')\partial_{r'} F_i(r')}\, dr' \right). \qquad (16)$$

Further simplifications done for Eq. (8) are applicable only to this particular problem and are impossible in the general case. This generalized equation can be used to describe, e.g., stable solutions for systems with several neuron and synapse types, in particular networks including inhibitory neurons. In this setting, the interaction between several bumps can exhibit more complex behavior than in the case of non-plastic synapses [12]. This equation is similar but not equivalent to an equation describing a one-component reaction-diffusion system (for only one i this mapping is exact). Still, a similar analysis of the existence of stable and metastable solutions, as presented for Eq. (5), is possible for this more general case. Preliminary results indicate that associative learning and memory can persist even if the activity is restored to the baseline level, similar as in [22]. In contrast to classical models of associative memory, such as fully connected Hopfield networks and Boltzmann machines [7], our formalism allows the study of spatially extended representations of earlier presented, learned objects.

Instead of propagating the activity in a feed-forward network from one layer to the next, we may consider a time-continuous system that is recurrently connected. With the leak term $-u/\tau_m$, the evolution of activity of such a system is described by

$$\partial_t u_t(\tilde{x}) = -\tau_m^{-1} u_t(\tilde{x}) + \sum_{x=\tilde{x}-(K-1)/2,\ x\neq\tilde{x}}^{\tilde{x}+(K-1)/2} w_t(\tilde{x},x) r_t(x), \quad (17)$$

where the lower index t denotes time point. The stationary solutions satisfy the equation

$$u_x = \sum_{x=\tilde{x}-(K-1)/2,\ x\neq\tilde{x}}^{\tilde{x}+(K-1)/2} \tau\left[w_0 + \frac{\gamma}{\alpha} f(u_x) f(u_{\tilde{x}}) \right] f(u_x), \quad (18)$$

which, after diffusion approximation of the sum, is equivalent to Eq. (5) with parameters $\tau\gamma$, τw_0, and $K-1$ instead of γ, w_0, and K. Hence, the presented results generalize to stationary solutions in recurrent networks.

ACKNOWLEDGMENTS

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