Bloch Waves, Periodic Feature Maps, and Cortical Pattern Formation

Paul C. Bressloff

Department of Mathematics, University of Utah, Salt Lake City, Utah 84112

Perturbation methods are used to solve the eigenvalue problem for cortical pattern formation in the presence of long-range neural connections. Such connections have a crystallinelike structure that breaks Euclidean symmetry to the discrete symmetry of a planar lattice group. Conditions for marginal stability are derived with the associated eigenmodes identified as Bloch waves.

One of the major simplifying assumptions in most large-scale models of cortical tissue is that the interactions between cell populations are invariant under the action of the Euclidean group of rigid body motions in the plane. Euclidean symmetry plays a key role in determining the types of activity patterns that can be generated spontaneously in these cortical networks. (For a review, see Ref. [1].) However, the assumptions of homogeneity and isotropy are no longer valid when the detailed microstructure of the cortex is taken into account. In fact, the cortex has a distinctly crystallinelike structure at the mm length scale. This is exemplified by the distribution of cytochrome oxidase (CO) blobs in primary visual cortex (V1). These regions, which are about 0.2 mm in diameter and about 0.4 mm apart, coincide with cells that are more metabolically active and hence richer in their levels of CO [2]. Moreover, the distribution of the CO blobs is correlated with a number of periodically repeating feature maps in which local populations of neurons respond preferentially to stimuli with particular properties such as orientation, spatial frequency, and left/right eye (ocular) dominance [3]. It has thus been suggested that the CO blobs are the sites of functionally and anatomically distinct channels of visual processing [4,5].

How does the periodic structure of visual cortex manifest itself anatomically? Two cortical circuits have been fairly well characterized. There is a local circuit operating at submillimeter dimensions in which cells make connections with most of their neighbors in a roughly homogeneous and isotropic fashion [6]. The other circuit operates over a range of several millimeters and is mediated by the laterally spreading patchy connectional fields made by pyramidal neurons in the superficial layers of V1. By matching anatomical projections with optically imaged feature maps, it has been shown that these lateral connections, which are broken into discrete patches with a very regular size and spacing [7–9], tend to link neurons having common functional properties as determined, for example, by their proximity to CO blobs [10–12].

In this Letter, we investigate how the periodic structure of lateral interactions, which is assumed to be correlated with the distribution of CO blobs, affects the large-scale dynamics of the cortex. In particular, we show how pertur-bation methods familiar from the analysis of the Schrödinger equation in a weak periodic potential [13] can be used to solve the eigenvalue problem for cortical pattern formation in the presence of periodically modulated long-range connections, with the resulting marginally stable eigenmodes identified as Bloch waves.

Our starting point is to treat a cortical layer of V1 as a continuous two-dimensional medium evolving according to the rate equation [1,14]

$$\frac{\partial a(\mathbf{r}, t)}{\partial t} = -\alpha a(\mathbf{r}, t) + \int_{\mathbf{R}^2} w(\mathbf{r} \mid \mathbf{r}')\sigma[a(\mathbf{r}', t)]d\mathbf{r}' + h(\mathbf{r}). \tag{1}$$

The scalar field $a(\mathbf{r}, t)$ represents the local activity of a population of (excitatory and inhibitory) neurons at cortical position $\mathbf{r} = (x, y) \in \mathbf{R}^2$ at time t, α is a decay rate (associated with membrane leakage currents or synaptic currents), $h(\mathbf{r})$ is an external input, and the distribution $w(\mathbf{r} \mid \mathbf{r}')$ is the strength of connections from neurons at $\mathbf{r}'$ to neurons at $\mathbf{r}$. The nonlinear firing-rate function σ is assumed to be a smooth monotonically increasing function of the form $\sigma(z) = 1/[1 + e^{-\gamma(z-\zeta)}]$ for constants γ and ζ. The weight distribution w is decomposed into local and long-range parts (see also Ref. [15]) according to

$$w(\mathbf{r} \mid \mathbf{r}') = W(|\mathbf{r} - \mathbf{r}'|) + \varepsilon w_{\text{lat}}(\mathbf{r} \mid \mathbf{r}'), \tag{2}$$

where W represents the local connections with $|\mathbf{r} - \mathbf{r}'| = \sqrt{(x - x')^2 + (y - y')^2}$ the Euclidean distance between two points in the cortical plane, w_{lat} represents the distribution of excitatory lateral connections, and ε is a coupling parameter. Experimentally, it is found that the lateral connections modulate rather than drive V1 activity [9], suggesting that $|\varepsilon|$ is small. The sign of ε determines whether the lateral connections have a net excitatory or inhibitory effect.

Motivated by the anatomy highlighted in the introduction, we assume that there exists a set of CO blobs arranged on a regular planar lattice $\mathcal{L}$ generated by two linearly independent vectors $\boldsymbol{\ell}_1$ and $\boldsymbol{\ell}_2$: $\mathcal{L} = \{m_1\boldsymbol{\ell}_1 + m_2\boldsymbol{\ell}_2 : m_1, m_2 \in \mathbf{Z}\}$. The lattice spacing $L = |\boldsymbol{\ell}_1| = |\boldsymbol{\ell}_2|$ is taken to be of the order of 0.5 mm. Let θ be the angle between the two basis vectors $\boldsymbol{\ell}_1$ and $\boldsymbol{\ell}_2$. We can then distinguish three

types of lattice depending on the value of θ: square ($\theta = \pi/2$), rhombic ($0 < \theta < \pi/2$, $\theta \neq \pi/3$), and hexagonal ($\theta = \pi/3$). It is further assumed that the preference of a cell for a particular stimulus feature such as orientation is determined by its position relative to this lattice. We then take the local connections W to have a spread covering approximately a single lattice spacing L so that they are broadly tuned with respect to feature preferences, whereas the lateral connections w_{lat} are taken to be narrowly tuned and to couple cells with similar feature preferences in distinct hypercolumns (defined as a fundamental domain of the lattice $\mathcal{L}$). This is illustrated in a one-dimensional version of the model in Fig. 1

An interesting recent experimental finding is that some cells located within intermediate distances from CO blobs have very little in the way of lateral connections [12] thus leading to an effective reduction in connectivity at the population level. This suggests that there is a periodic variation in the strength of the lateral coupling; that is,

$$w_{\text{lat}}(\mathbf{r} \mid \mathbf{r}') = \mathcal{D}(\mathbf{r})J(\mathbf{r} - \mathbf{r}'), \qquad (3)$$

where $\mathcal{D}$ is a doubly periodic function; that is, $\mathcal{D}(\mathbf{r} + \ell) = \mathcal{D}(\mathbf{r})$ for all $\ell \in \mathcal{L}$, and $J(\mathbf{r})$ incorporates the condition that long-range connections only link cells with similar feature preferences as determined by their location relative to CO blobs. The latter condition is implemented by setting $J(\mathbf{r}) = \sum_{\ell \in \mathcal{L}} J_\ell \Theta[\mathcal{P}_0 - \mathcal{P}_\ell(\mathbf{r})]$, where (i) $\Theta(x) = 1$ for $x > 0$ and $\Theta(x) = 0$ for $x < 0$, and (ii) $\mathcal{P}_\ell(\mathbf{r}) = |\mathbf{r} - \ell|$ if $|\mathbf{r} - \ell| < |\mathbf{r} - \ell'|$ for all $\ell' \neq \ell$ and is equal to L otherwise. The parameter $\mathcal{P}_0$, $0 < \mathcal{P}_0 < L/2$, determines the patch size and J_ℓ represents the decay in the strength of patches with lattice separation ℓ. An example of w_{lat} is shown in Fig. 2.

Suppose that there exists a homogeneous fixed point solution of Eq. (1), $a(\mathbf{r}, t) = a_0$. (For the given nonlinearity σ, at least one fixed point exists in the case of homogeneous weights w and a uniform input h. Such a fixed point persists in the presence of weak inhomogeneties.) Setting $a(\mathbf{r}, t) = a_0 + e^{\lambda t}a(\mathbf{r})$ and linearizing about the fixed point leads to the eigenvalue equation

$$\lambda a(\mathbf{r}) = -a(\mathbf{r}) + \mu \int_{\mathbf{R}^2} w(\mathbf{r}|\mathbf{r}')a(\mathbf{r}')d\mathbf{r}', \qquad (4)$$

where $\mu = \sigma'(a_0)$ and we have fixed the time scale by setting $\alpha = 1$. Since the weight distribution w is bounded, it follows that when the network is in a low activity state a_0 such that $\mu = \sigma'(a_0) \approx 0$, any solution of Eq. (4) satisfies $\text{Re}\lambda < 0$ and the fixed point is linearly stable. However, when the excitability of the network is increased, either through the action of some hallucinogen or through external stimulation, μ increases. This can induce an instability leading to the formation of spontaneous cortical activity patterns. We shall derive conditions for the onset of such an instability for the weight distribution (2).

First consider the case of zero lateral connections such that $w(\mathbf{r} \mid \mathbf{r}') = W(|\mathbf{r} - \mathbf{r}'|)$. The distribution w is then invariant with respect to the Euclidean group, and the eigenmodes are in the form of plane waves $a_{\mathbf{k}}(x) = e^{i\mathbf{k}\cdot\mathbf{r}}$ with wave number $\mathbf{k}$. Substitution into Eq. (4) shows that the corresponding eigenvalues are $\lambda(k) = -1 + \mu\tilde{W}(k)$, where $k = |\mathbf{k}|$ and $\tilde{W}(k)$ is the Fourier transform of $W(\mathbf{r})$; that is, $\tilde{W}(k) = \int_{\mathbf{R}^2} W(\mathbf{r})e^{-i\mathbf{k}\cdot\mathbf{r}}d\mathbf{r}$. Assume that W consists of a mixture of short-range excitation and longer-range inhibition (see Fig. 2) such that $\tilde{W}(k)$ is bounded with a global positive maximum at $k = k_c \neq 0$. Then, for sufficiently small μ, $\lambda(k) < 0$ for all k and the zero solution is stable. However, as μ increases, the zero solution destabilizes at the critical value $\mu_c = \alpha/\tilde{W}(k_c)$ due to excitation of plane waves with critical wave number k_c. Rotation symmetry implies that the space of marginally stable states is infinite dimensional; that is, all plane waves with wave vectors $\mathbf{k}$ lying on the critical circle $|\mathbf{k}| = k_c$ are allowed.

If the lateral connections are now switched on, continuous Euclidean symmetry is restricted to the discrete symmetry group $\Gamma_{\mathcal{L}}$ of the lattice $\mathcal{L}$, since w is now doubly periodic with $w(\mathbf{r} + \ell \mid \mathbf{r} + \ell) = w(\mathbf{r} \mid \mathbf{r}')$ for all $\ell \in \mathcal{L}$. It then follows that solutions of Eq. (4) are in the form of Bloch waves [13]: $a_{\mathbf{k}}(\mathbf{r}) = e^{i\mathbf{k}\cdot\mathbf{r}}u_{\mathbf{k}}(\mathbf{r})$ with $u_{\mathbf{k}}(\mathbf{r} + \ell) = u_{\mathbf{k}}(\mathbf{r})$ for all $\ell \in \mathcal{L}$. In order to show this, we introduce the Fourier series expansions $\mathcal{D}(\mathbf{r}) = \sum_{\mathbf{q}} \mathcal{D}_{\mathbf{q}}e^{i\mathbf{q}\cdot\mathbf{r}}$ for $\mathbf{q} = \sum_{j=1,2} 2\pi n_j \hat{\ell}_j$ and $a(\mathbf{r}) = \Lambda^{-1}\sum_{\mathbf{k}} a_{\mathbf{k}}e^{i\mathbf{k}\cdot\mathbf{r}}$ for $\mathbf{k} = \sum_{j=1,2} \frac{2\pi m_j}{N}\hat{\ell}_j$, where $\hat{\ell}_j$, $j = 1, 2$, are the generators of the reciprocal lattice $\hat{\mathcal{L}}$ such that $\hat{\ell}_i \cdot \ell_j = \delta_{i,j}$. We have
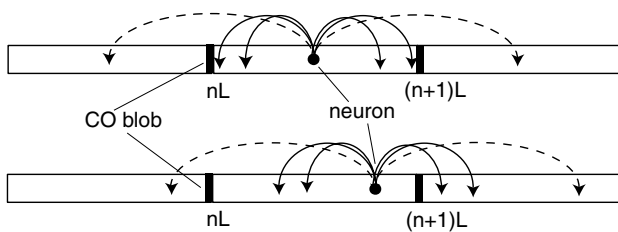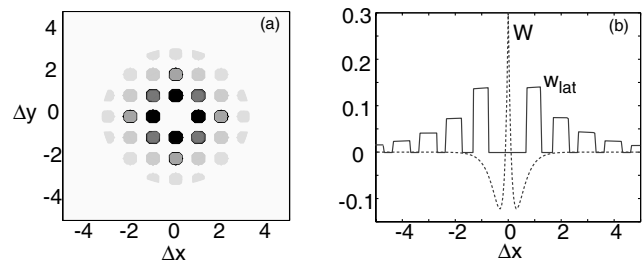

FIG. 1. One-dimensional periodic lattice of CO blobs. Neurons are coupled by broadly tuned local connections (solid curves) and narrowly tuned long-range horizontal connections (dashed curves).

FIG. 2. (a) Plot of patchy lateral connections $w_{\text{lat}}(\mathbf{r} \mid \mathbf{r}')$ on a square lattice as a function of cortical separation $\Delta\mathbf{r} = \mathbf{r} - \mathbf{r}'$ (in units of the lattice spacing L). The strength of the connections is indicated using gray scale. (b) Cross section of w_{lat} along the x axis together with an example of a local Mexican hat distribution W.

also imposed the periodic boundary condition $a(\mathbf{r} + N\ell_j) = a(\mathbf{r})$, $j = 1, 2$, for some integer $N \gg 1$ and set $\Lambda = (NL)^2$. Equation (4) then reduces to the form

$$[\lambda + \alpha - \mu \tilde{W}(k)]a_{\mathbf{k}} = \varepsilon \sum_{\mathbf{q}} \mathcal{V}_{\mathbf{q}}(\mathbf{k})a_{\mathbf{k}-\mathbf{q}}, \quad (5)$$

where $\mathcal{V}_{\mathbf{q}}(\mathbf{k}) = \tilde{J}(\mathbf{k} - \mathbf{q})\mathcal{D}_{\mathbf{q}}$ and $\tilde{J}(\mathbf{k})$ is the Fourier transform of $J(\mathbf{r})$. Equation (5) implies that the lateral interactions only couple together those coefficients $a_{\mathbf{k}}, a_{\mathbf{k}-\mathbf{q}}, a'_{\mathbf{k}-\mathbf{q}}, \ldots$ whose wave vectors differ by a reciprocal lattice vector. Hence, we obtain Bloch waves with $u(\mathbf{r})$ the periodic function $u(\mathbf{r}) = \sum_{\mathbf{q}} a_{\mathbf{k}-\mathbf{q}} e^{-i\mathbf{q}\cdot\mathbf{r}}$.

It is generally not possible to find exact solutions of the eigenvalue equation (5). However, we can proceed by carrying out a perturbation expansion with respect to the small coupling parameter ε along analogous lines to solving the Schrödinger equation in a weak periodic potential [13]. Let k_c be the critical wave number for a pattern forming instability when $\varepsilon = 0$. We also define $\mathcal{N}_\varepsilon(k_c)$ to be a small neighborhood of the critical circle $|\mathbf{k}| = k_c$. We then have to distinguish between two scenarios based on whether or not the following degeneracy condition holds: there exists a reciprocal lattice vector $\mathbf{Q}$ such that

$$|\tilde{W}(|\mathbf{k}|) - \tilde{W}(|\mathbf{k} - \mathbf{Q}|)| = \mathcal{O}(\varepsilon), \qquad \mathbf{k} \in \mathcal{N}_\varepsilon(k_c), \quad (6)$$

and $|\tilde{W}(|\mathbf{k}|) - \tilde{W}(|\mathbf{k} - \mathbf{q}|)| \gg \varepsilon$ for all $\mathbf{q} \neq \mathbf{Q}$. Note that the exact degeneracy condition $\tilde{W}(|\mathbf{k}|) = \tilde{W}(|\mathbf{k} - \mathbf{Q}|)$ is only satisfied if $|\mathbf{k}| = |\mathbf{k} - \mathbf{Q}|$. This means that $\mathbf{k}$ must lie on the perpendicular bisector of the line joining the origin of the reciprocal lattice $\hat{\mathcal{L}}$ to the lattice point $\mathbf{Q}$; that is, it lies on the boundary of a Brillouin zone [13].

First, suppose that Eq. (6) does not hold; that is, if $\mathbf{k} \in \mathcal{N}_\varepsilon(k_c)$, then $|\tilde{W}(|\mathbf{k}|) - \tilde{W}(\mathbf{k} - \mathbf{q})| \gg \varepsilon$ for all $\mathbf{q} \in \hat{\mathcal{L}}, \mathbf{q} \neq 0$. This occurs, for example, if the critical circle lies well within the first Brillouin zone. A standard perturbation calculation then shows that to first order in ε the eigenmode $u_{\mathbf{k}}(\mathbf{r}) = 1$ and $\lambda = -1 + \mu[\tilde{W}(|\mathbf{k}|) + \varepsilon \mathcal{V}_0(\mathbf{k})]$. To leading order in ε, the marginally stable modes will be those modes on the critical circle that maximize (minimize) the term $\mathcal{V}_0(\mathbf{k})$ for $\varepsilon > 0$ (for $\varepsilon < 0$). Since $\mathcal{V}_0(\mathbf{k})$ is invariant with respect to the corresponding lattice group $\Gamma_{\mathcal{L}}$, a particular wave vector $\mathbf{k}^*$ on the critical circle will typically be selected together with all modes generated by discrete rotations of the lattice. (We ignore accidental degeneracies here). This is illustrated in Fig. 3(a) for the square lattice. The eigenmodes will thus be of the form $a(\mathbf{r}) = \sum_{j=1,\ldots N} u_j e^{i\mathbf{k}_j \cdot \mathbf{r}} + \text{c.c.}$ Here $N = 2$ for the square lattice with $\mathbf{k}_1 = \mathbf{k}^*$ and $\mathbf{k}_2 = R_{\pi/2}\mathbf{k}^*$, where R_θ denotes rotation through an angle θ. Similarly, $N = 3$ for the hexagonal lattice with $\mathbf{k}_1 = \mathbf{k}^*$, $\mathbf{k}_2 = R_{2\pi/3}\mathbf{k}^*$, and $\mathbf{k}_3 = R_{4\pi/3}\mathbf{k}^*$.

Now suppose that the degeneracy condition (6) is satisfied for some $\mathbf{Q} \in \hat{\mathcal{L}}$, which implies that the critical circle is close to a Brillouin zone boundary [see Fig. 3(b)]. Then, to first order in ε, Eq. (5) reduces to a
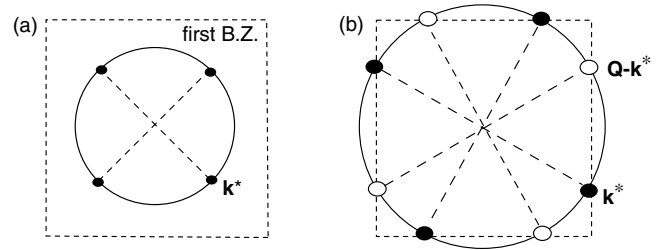

FIG. 3. Selected wave vectors on the critical circle for a square lattice. (a) Nondegenerate case: the critical circle lies well within the first Brillouin zone. (b) Degenerate case: the critical circle intersects the border of the first Brillouin zone, and there is a doubling up of the marginally stable modes.

pair of equations for the coefficients $a_{\mathbf{k}}$ and $a_{\mathbf{k}-\mathbf{Q}}$:

$$\begin{pmatrix} \lambda - E(\mathbf{k}) & \varepsilon \mathcal{V}_{\mathbf{Q}}(\mathbf{k}) \\ \varepsilon \mathcal{V}_{-\mathbf{Q}}(\mathbf{k} - \mathbf{Q}) & \lambda - E(\mathbf{k} - \mathbf{Q}) \end{pmatrix} \begin{pmatrix} a_{\mathbf{k}} \\ a_{\mathbf{k}-\mathbf{Q}} \end{pmatrix} = 0, \quad (7)$$

where $E(\mathbf{k}) = -1 + \mu[\tilde{W}(|\mathbf{k}|) + \varepsilon \mathcal{V}_0(\mathbf{k})]$. Assume for the moment that the exact degeneracy condition $\tilde{W}(|\mathbf{k}|) = \tilde{W}(\mathbf{k} - \mathbf{Q})$ holds so that $\mathbf{k}$ is on a Brillouin zone boundary. As a further simplification, let $\tilde{J}(\mathbf{k} - \mathbf{q}) = \tilde{J}(\mathbf{k})$ for all $\mathbf{q} \in \hat{\mathcal{L}}$ so that $\mathcal{V}_{-\mathbf{Q}}(\mathbf{k} - \mathbf{Q}) = \mathcal{V}_{\mathbf{Q}}(\mathbf{k})$. (This is a good approximation when the patch size $\mathcal{P}_0$ is small). The above matrix equation then has solutions of the form

$$\lambda_\pm(\mathbf{k}) = -1 + \mu\{\tilde{W}(|\mathbf{k}|) + \varepsilon[\mathcal{V}_0(\mathbf{k}) \pm \mathcal{V}_{\mathbf{Q}}(\mathbf{k})]\}, \quad (8)$$

with $a_{\mathbf{k}-\mathbf{Q}} = \pm a_{\mathbf{k}}$. Thus there is a splitting into even and odd eigenmodes $u_{\mathbf{k}}^\pm(\mathbf{r}) = e^{i\mathbf{k}\cdot\mathbf{r}} \pm e^{i(\mathbf{k}-\mathbf{Q})\cdot\mathbf{r}}$. (If $\mathbf{k}$ is close to, but not on, the Brillouin zone boundary, there will be a slight mixing between the even and odd eigenmodes—this will not modify our conclusions significantly.) Let $\mathbf{k}_\pm$ denote global maxima of the functions $\lambda_\pm(\mathbf{k})$ and set $\mathbf{k}^* = \mathbf{k}_+$ if $\lambda_+(\mathbf{k}_+) > \lambda_-(\mathbf{k}_-)$, and $\mathbf{k}^* = \mathbf{k}_-$ otherwise. It follows that the marginally stable eigenmodes will be of the approximate form $a(\mathbf{r}) = \sum_{j=1,\ldots N} z_j u_{\mathbf{k}_j}^\pm(\mathbf{r}) + \text{c.c.}$ with $\mathbf{k}_1 = \mathbf{k}^*$ and $\mathbf{k}_j, j = 2, \ldots, N$, related to $\mathbf{k}^*$ by discrete rotations of the lattice. Even (+) modes will be selected when $\mathbf{k}^* = \mathbf{k}^+$ and odd (−) modes when $\mathbf{k}^* = \mathbf{k}_-$.

We conclude from the above analysis that the crystal-linelike structure of V1, as manifested by a periodicity in the distribution of lateral connections, can have a major effect on the types of spontaneous activity patterns generated in the cortex: (i) Doubly periodic patterns such as rolls, squares, and hexagons occur through an explicit breaking of continuous Euclidean symmetry by a physical lattice of CO blobs. Such activity patterns are of particular interest, since they provide a possible explanation for the occurrence of certain basic types of geometric visual hallucinations [16,17]. (Note that in Euclidean symmetric models of cortical pattern formation, the double periodicty of the solutions is imposed by hand as a mathematical simplification rather than reflecting the existence of a real lattice.) (ii) There is an analog of "Bragg scattering"
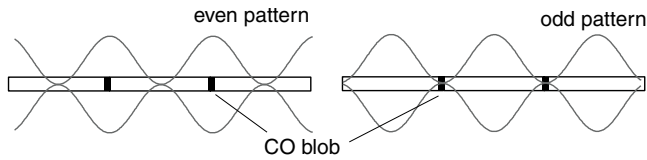
FIG. 4. Even and odd eigenmodes localized around blob and interblob regions.

[13] within the context of neural pattern formation whereby for certain critical wave numbers k_c the resulting activity patterns are localized around either CO blobs or around interblob regions as illustrated in Fig. 4. This follows from the structure of the even and odd solutions of Eq. (7), which are in the form of standing waves whose amplitudes vary as $\cos(\mathbf{Q} \cdot \mathbf{r}/2)$ and $\sin(\mathbf{Q} \cdot \mathbf{r}/2)$, respectively.

More generally, our work shows how techniques familiar in the study of crystalline solids can be used to analyze the large-scale spontaneous dynamics of the cortex. We have focused on the distribution of CO blobs, since this is one candidate structure for breaking the translation symmetry of cortex. However, the same methods could also be applied to other latticelike structures such as the distribution of orientation singularities. (The CO blobs appear to coincide with about half the singularities, namely, those associated with low spatial frequencies [3].) We note that these various lattices have substitutional and topological disorder, both of which need to be taken into account in a more detailed study. Understanding the spontaneous behavior of the cortex may also provide insights into the stimulus evoked response properties of the cortex. Indeed, recent optical imaging experiments have revealed that the cortex exhibits activity patterns in the absence of external visual stimulation that resemble those induced by a single oriented stimulus [18]. Finally, it would be interesting to investigate how the periodic structures highlighted in this Letter actually develop in the cortex, and subsequently influence the development of other cortical structures. Perhaps such processes lead to a match between the critical wavelength $2\pi/k_c$ of cortical activity patterns with the lattice spacing L through the self-consistent generation of the even and odd patterns shown in Fig. 4.

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