

## Symmetry Induced Coupling of Cortical Feature Maps

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The mammalian visual cortex maps *retinal position (retinotopy)* and *orientation preference (OP)* across its surface. Simultaneous measurements *in vivo* suggest that positive correlation exists between the location of dislocations in these two maps, contradicting the predictions of classical dimension reduction models. Model symmetries exert a significant influence on pattern development. However, classical models for cortical map formation have inappropriate symmetry properties. By applying equivariant bifurcation theory we derive symmetry induced, model independent coupling of the OP and retinotopic maps and show that this coupling replicates observations.

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In the mammalian visual cortex, the activities of individual neurons signal the retinal location and angle of oriented elements in the visual field (bars, edges, or gratings) [1,2]. These activities are organized in topographic maps. The development of such maps may be viewed as a problem of pattern formation in a two-dimensional neural net [3–6]. The development of retinotopic and orientation preference (OP) maps appears to be coupled in as much as simultaneous measurements of both maps show correlations in their structure [7]. The classic dimension reduction model predicts that dislocations in OP should avoid those in retinotopy [8], while the experiments of Das and Gilbert indicate just the opposite [7]. Pattern formation in models of spontaneous neural activity is influenced by symmetries inherent in the structure of the interactions between orientation selective neurons [9–11]. The coupling of pattern formation processes in multiple maps with symmetries is a straightforward extension of the scalar case, but has not previously been applied to the problem of cortical map development. In this Letter we show that the treatment of cortical map development in the framework of equivariant bifurcation theory [12] leads naturally to symmetry induced coupling between different cortical feature maps and can account for the observed correlations between the retinotopic and OP maps.

We represent the population tuning for orientation by the vector field

$$\chi(\mathbf{x}) = q(\mathbf{x})[\cos(2\phi(\mathbf{x})), \sin(2\phi(\mathbf{x}))], \quad (1)$$

where  $0 \leq \phi(\mathbf{x}) \leq \pi$  denotes the preferred stimulus orientation at cortical location  $\mathbf{x}$ . The magnitude  $q(\mathbf{x})$  reflects the strength of the tuning;  $q = 0$  indicates a rotationally invariant response. The organization of the OP map is characterized by local patches within which nearby cells have similar preferences and across which preferences change gradually, interspersed with “singularities” (spaced typically  $\approx 0.56$  mm apart in the cat [7]

and  $\approx 0.35$  mm in the monkey [13]) at which all preferences converge and “fractures” or line segments across which preferences shift abruptly by  $\pi/2$  [2,14]. The map from cortical location  $\mathbf{x}$  to retinal position  $\mathbf{r}(\mathbf{x})$  is smooth and linear on a scale from 0.5 to 5 mm in the cortex [15,16] and is approximately isotropic (neglecting the effects of superposed projections from the two eyes). On a scale from 50–500  $\mu\text{m}$  the retinotopic map shows deviations from the smooth local average, and the sites of these distortions correlate positively with the singularities in the orientation map [7]. We therefore assume the existence of a coarse retinotopic map given by an affine transformation from cortical to visual field coordinates, on which a small deviation  $|\mathbf{s}(\mathbf{x})| \ll 1$  is superimposed:

$$\mathbf{r}(\mathbf{x}) = \mathbf{x} + \mathbf{s}(\mathbf{x})$$

(with appropriately chosen units for  $\mathbf{x}$  and  $\mathbf{r}$ ).

We consider the joint development of the OP and retinotopic maps as a family of steady states that branch from an isotropic homogeneous state. We assume a dynamical system  $\dot{\mathbf{v}} = F[\mathbf{v}]$ ,  $\mathbf{v} = [\mathbf{s}; \chi]^T \in \mathbb{R}^4$ , describing the joint development of  $\chi(\mathbf{x})$  and  $\mathbf{s}(\mathbf{x})$ , which is equivariant under the action of the Euclidean group  $\mathbf{E}_2 = \mathbf{T}^2 \rtimes \mathbf{O}_2$  generated by rotations ( $\mathcal{R}_\psi$ ), reflection in the cortical  $[1, 0]$  axis ( $\kappa$ ), and planar translations ( $\mathbf{T}^2 = \mathcal{T}_{t_1, t_2}$ ). The action of rotation by  $\psi$  is doubled on the OP map, in accordance with Eq. (1):

$$\text{Rot.}\psi: \begin{bmatrix} \mathbf{s}(\mathbf{x}) \\ \chi(\mathbf{x}) \end{bmatrix} \rightarrow \begin{pmatrix} \mathcal{R}_\psi & \\ & \mathcal{R}_{2\psi} \end{pmatrix} \begin{bmatrix} \mathbf{s}(\mathcal{R}_{-\psi}\mathbf{x}) \\ \chi(\mathcal{R}_{-\psi}\mathbf{x}) \end{bmatrix}. \quad (2)$$

There is no independent rotational symmetry for  $\chi(\mathbf{x})$  or  $\mathbf{s}(\mathbf{x})$  alone. It is this equivariance under a common action that forces the coupling of orientation and retinotopy during development. This symmetry induced coupling is entirely natural but has been overlooked in previous models. Reflection in the  $x$  axis acts in the same fashion on both vector fields:

$$\text{Reflection in } [1, 0]^T: \begin{bmatrix} \mathbf{s}(\mathbf{x}) \\ \boldsymbol{\chi}(\mathbf{x}) \end{bmatrix} \rightarrow \begin{pmatrix} \kappa & \\ & \kappa \end{pmatrix} \begin{bmatrix} \mathbf{s}(\kappa\mathbf{x}) \\ \boldsymbol{\chi}(\kappa\mathbf{x}) \end{bmatrix}, \quad (3)$$

where  $\kappa = \text{diag}(1, -1)$  is a  $2 \times 2$  reflection matrix.

In addition to Euclidean equivariance, we presume the dynamical system  $F$  has a Euclidean invariant homogeneous steady state given by  $q \equiv 0$  (no orientation tuning) and  $s \equiv 0$  (strictly uniform retinotopy  $\mathbf{r}(\mathbf{x}) \equiv \mathbf{x}$ ) that loses stability to spatial perturbations at a critical spatial frequency  $|k| \approx 2\pi(300 \mu\text{m})^{-1}$  corresponding to the typical length scale seen in cortical patterns. Experimentally, orientation tuning is observed to be nearly isotropic in the early stages of cortical development [17,18]; similarly, immature receptive fields show broader spatial tuning than adult receptive fields [19]. Because both maps are influenced by the spatial distribution of afferent fibers [20], and because orientation and spatial tuning sharpen together [21], it is reasonable to expect coordinated pattern formation in both maps. The common length scale may arise from the development of intracortical ‘‘Mexican hat’’ lateral connections believed to underlie the formation of cortical activity patterns [6].

In the case of a single vector field the pattern emerging from the isotropic equilibrium comprises plane waves of the form  $\mathbf{u} \exp(i\mathbf{k}\mathbf{x}) + \text{c.c.}$ , due to translation symmetry [10]. Each such subspace splits into even and odd isotypic components corresponding to irreducible group representations in which reflection in the axis parallel to  $\mathbf{k}$  acts as  $\pm 1$ . The linearization of the dynamics about the isotropic fixed point,  $dF$ , commutes with the action of the underlying symmetry. Consequently its null eigenvectors will

lie in an irreducible representation, selecting a planform from either the even or the odd null space. In the case of two coupled vector fields, if each contains an isomorphic irreducible representation of the group action, then the null eigenvector will generically contain nonzero components in both subspaces. In the case of the OP and retinotopic distortion maps, we obtain coordinated multi-map planforms combining, respectively, the even or odd subspaces of each vector field. Furthermore the kernel of the linearization decomposes into isotypic components under the action of the group and the linearization leaves invariant each component. In each isotypic component, each null eigenvector transforms in the same fashion under the action of the group (*symmetry-adapted basis vectors* [22]), thereby fixing the relative phase of the component plane waves, up to a model dependent change of sign.

Figure 1 depicts typical eigenvectors in the even and odd null spaces of  $dF$ . OP ( $\boldsymbol{\chi}$ ) and retinotopic distortion ( $\mathbf{s}$ ) plane waves in the direction  $\mathbf{k}_\psi = |\mathbf{k}|[\cos\psi, \sin\psi]^T$  are given by

$$\begin{aligned} \mathbf{s}_+(\psi) &= -i\mathbf{k}_\psi e^{i\mathbf{k}_\psi \mathbf{x}} + \text{c.c.}, \\ \boldsymbol{\chi}_+(\psi) &= \mathbf{k}_{2\psi} e^{i\mathbf{k}_\psi \mathbf{x}} + \text{c.c.}, \\ \mathbf{s}_-(\psi) &= -i\mathbf{k}_{\psi+(\pi/2)} e^{i\mathbf{k}_\psi \mathbf{x}} + \text{c.c.}, \\ \boldsymbol{\chi}_-(\psi) &= \mathbf{k}_{2\psi+(\pi/2)} e^{i\mathbf{k}_\psi \mathbf{x}} + \text{c.c.}, \end{aligned} \quad (4)$$

where  $\pm$  denotes the even or odd subspace, respectively. The particular form of the even and odd paired wave forms is dictated by the group action (2).

At the bifurcation point, rotational symmetry generates an infinite-dimensional null space of the linearized

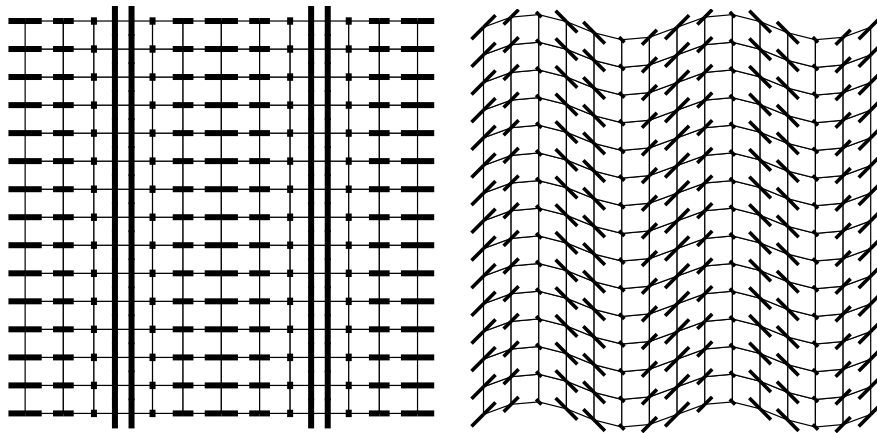


FIG. 1. Even and odd isotypic components for coupled  $\pi$ -periodic and  $2\pi$ -periodic vector fields. The mesh grid indicates the retinotopic map from regularly spaced loci in cortical coordinates  $\mathbf{x}$  to displaced visuotopic coordinates  $\mathbf{r}(\mathbf{x}) = \mathbf{x} + \mathbf{s}(\mathbf{x})$ . The oriented bars indicate the direction of OP; their length denotes the strength of OP. The Euclidean group action uniquely couples OP and retinotopy up to a shift of  $\pi$  in the relative phase along the wave vector direction  $\mathbf{k}$  (in these examples  $\mathbf{k} = [1, 0]^T$ ). Left panel: Even isotypic component. The retinotopic distortion vector  $\mathbf{s}(\mathbf{x})$  lies parallel to  $\mathbf{k}$ , creating a ‘‘compression wave’’ pattern. The preferred orientation lies alternately parallel and orthogonal to  $\mathbf{k}$ . Right panel: Odd isotypic component. The retinotopic distortion vector  $\mathbf{s}(\mathbf{x})$  lies orthogonal to  $\mathbf{k}$ , creating a ‘‘transverse wave’’ pattern. The preferred orientation alternates between oblique angles  $\pm\pi/4$  with respect to  $\mathbf{k}$ .

dynamics  $dF$ . As in the case of planar pattern formation in a convecting fluid we restrict ourselves to solutions with the symmetry of a lattice. Thus our irreducible solution spaces become six dimensional (hexagonal lattice) or four dimensional (square and rhombic lattices). The equivariant branching lemma guarantees the existence of solutions with the symmetry of *axial subgroups* of the lattice symmetry, i.e., those subgroups with one-dimensional fixed-point subspaces [12]. The axial subgroups for the even and odd subspaces under the action of cortical symmetries, restricted to the different lattices, have been classified elsewhere [9,10]. The bifurcating solutions take the form

$$\mathbf{s}(\mathbf{x}) = \sum_j z_j \mathbf{s}_\pm(\psi_j), \quad \boldsymbol{\chi}(\mathbf{x}) = a \sum_j z_j \boldsymbol{\chi}_\pm(\psi_j), \quad (5)$$

where  $j \in \{1, 2\}$  for the square or rhombic and  $j \in \{1, 2, 3\}$  for the hexagonal lattice;  $\psi_1 = 0$ ,  $\psi_2 = 2\pi/3$  (hex),  $\pi/2$  (square), or  $\eta$  (rhombic) with  $0 < (\eta \neq \pi/3) < \pi/2$ ;  $\psi_3 = -2\pi/3$  for the hexagonal lattice; and  $a \in \mathbb{R}$  is a model dependent parameter fixed by the null eigenvector of  $dF$ . Changing the sign of  $a$  qualitatively changes the appearance of the resulting planforms but does not change the observed correlations between the orientation and retinotopic maps. The  $z_i$  are unitary complex numbers defining the different planforms; see Table I.

The stability of solutions corresponding to the different planforms generally depends on nonlinear terms up to the fifth order near the bifurcation point [10]. We consider only the linear coupling terms, forced by the symmetry of  $dF$ . There are eleven distinct axial subgroup solutions [9]. We consider only those planforms the OP maps of which are *topologically equivalent* to the physiologically observed maps, i.e., those exhibiting pinwheel singularities of topological degree  $\pm\pi$  only. Four of the 11 plan-

TABLE I. Axial subgroups and associated planforms topologically equivalent to those observed via optical imaging. For a full list of planforms see [9].  $C$  is the correlation coefficient of  $|\nabla[\phi(x)]|$  and  $\det(\partial\mathbf{r}/\partial\mathbf{x})$ . The vector  $\{z_j\}$  has three components for the hexagonal lattice and two for the rhombic and square lattices. For the even and odd rhombic planforms,  $C$  depends on the lattice angle  $\eta$ . For values of  $\eta$  giving plausible map patterns ( $\pi/5 < \eta < \pi/2$ ),  $C$  is usually positive (see text). Last row: superpositions of 256 combined OP and retinotopy plane waves of Gaussian distributed amplitude and uniformly distributed phase and direction [23] had a weak but significant bias towards positive values of  $C$ .

Parity	Lattice	Description	$[z_1, z_2, (z_3)]$	Correlation $C$
Odd	Hex	“Triangles”	$[i, i, i]$	+0.288
Odd	Hex	“Rectangles”	$[0, 1, -1]$	+0.106
Odd	Rhomb	“Rhombs”	$[1, 1]$	$\approx > 0$ (see text)
Even	Rhomb	“Rhombs”	$[1, 1]$	$\approx > 0$ (see text)
Neither	None	“Random”	See caption	$+0.010 \pm 0.032$

forms give qualifying OP patters: odd triangles and odd rectangles on the hexagonal lattice and both even and odd rhomb patterns on the rhombic lattice. The remaining planforms have either lattices of  $-\pi$  and  $+2\pi$  pinwheels, line singularities intersecting at saddle points, or no singularities; we do not consider these further.

Das and Gilbert simultaneously obtained a map of OP over a several square mm region of cat visual cortex via optical imaging of intrinsic cortical signals and measured the retinotopy of individual cell receptive-field centers via direct electrophysiological recordings [7]. By comparing the rate of change of OP and retinotopic coordinates between neighboring recording sites, they found a weak positive correlation between the relative rates of change of both variables. Subsequent attempts to determine the correlation of the OP map with retinotopic dislocations have yielded weak positive results [24] or null results on a coarser length scale [15].

For each planform generated by our analysis we numerically determined the preferred orientation  $\phi(\mathbf{x}) = (1/2)\tan^{-1}(\chi_2(\mathbf{x})/\chi_1(\mathbf{x}))$ , and the Jacobian  $J(\mathbf{x}) = \partial\mathbf{r}/\partial\mathbf{x}$ . The determinant  $M(\mathbf{x}) = \det(J(\mathbf{x}))$  gives an isotropic measure of the local rate of change of retinotopic position with respect to the cortical position. To compare our planforms with Das and Gilbert’s measurements we calculated the correlation coefficient between  $M$  and  $|\nabla\phi|$ :

$$C = \frac{\langle (|\nabla\phi| - \langle |\nabla\phi| \rangle)(M - \langle M \rangle) \rangle}{\sqrt{\langle (|\nabla\phi| - \langle |\nabla\phi| \rangle)^2 \rangle \langle (M - \langle M \rangle)^2 \rangle}}. \quad (7)$$

The value of  $C$  is independent of the model dependent sign of the factor  $a$  in Eqs. (5), since  $\nabla\phi = (\chi_1\nabla\chi_2 - \chi_2\nabla\chi_1)/(2|\boldsymbol{\chi}|^2)$  is even under  $\boldsymbol{\chi} \rightarrow -\boldsymbol{\chi}$ . Table I shows numerical evaluation of  $C$  for the planforms of interest, calculated using a  $100 \times 100$  grid corresponding to two wavelengths  $2\pi/|\mathbf{k}|$ . Consistent with the measurements of Das and Gilbert, all four planforms giving topologically appropriate pinwheel patterns have small but significant positive correlations ( $+10\%$  to  $+20\%$ ). Figure 2 shows combined OP and retinotopy planforms for three such planforms: the odd hexagonal triangle and rectangle patterns and the even rhomb-lattice planform for an intermediate value of  $\eta$  ( $\pi/4$ ). The value of  $C$  for the even and odd rhombic patterns varies with the lattice angle  $\eta$ . While all values of  $0 < \eta < \pi/2$  give  $\pm\pi$  singularities, the maps are only “cortexlike” in appearance for roughly  $0.2\pi < \eta < \pi/2$ . In this range the correlations range from  $-0.007$  to  $+0.026$  for even rhombs and from  $-0.036$  to  $+0.32$  for odd rhombs; and 77% of the even and 94% of the odd patterns have positive correlations.

We have shown how symmetries intrinsic to the development of the orientation preference and retinotopic maps induce a natural coupling between them. The application of equivariant bifurcation theory can correctly account

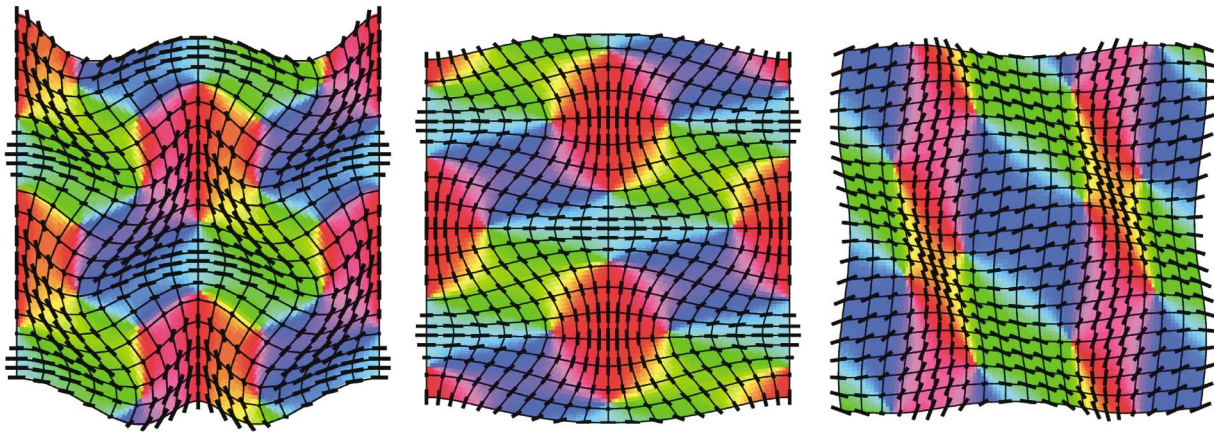


FIG. 2 (color). Three OP and retinotopy planforms predicted at a bifurcation point by the equivariant branching lemma. Left panel: triangular planform on hexagonal lattice, odd isotypic component. Combines OP singularities of topological degree  $\pm\pi$  and line singularities across which OP changes by  $\pi/2$ . Center panel: rectangular planform on hexagonal lattice, odd isotypic component. OP singularities of topological degree  $\pm\pi$  alternate sign with their nearest neighbors. Right panel: rhomb planform on rhombic lattice (with  $\eta = \pi/4$ ), even isotypic component. OP singularities of topological degree  $\pm\pi$  alternate sign with their nearest neighbors. Color code for OP: red = vertical, blue =  $+\pi/6$ , green =  $-\pi/6$ .

for the weak positive correlations between the OP and retinotopic maps observed experimentally [7,24]. Detailed derivation of a specific model for the dynamics  $F$  from an underlying biophysically realistic dynamics for the development of individual afferent fibers leads to a system with the appropriate symmetries [25]; in this case the value of the coupling parameter  $a$  is positive due to the imposition of constraints on the uniformity of the afferent weight distribution [26].

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