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Simultaneous constraints on pre- and post-synaptic cells couple cortical feature maps in a 2D geometric model of orientation preference

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The most prominent feature of mammalian striate cortex (V1) is the spatial organization of response preferences for the position and orientation of elementary visual stimuli. Models for the formation of cortical maps of orientation and 'retinotopic' position typically rely on a combination of Hebbian or correlation-based synaptic plasticity, and constraints on the distribution of synaptic weights. We consider a simplified model of orientation and retinotopic specificity based on the geometry of the feedforward synaptic weight distribution from an 'unoriented' layer of cells to a first weakly oriented layer. We model the feed-forward weight distribution as a system of planar Gaussian receptive fields each elongated in the direction matching the preferred orientation of the postsynaptic cell. Under the constraint of presynaptic weight normalization (each cell in the oriented layer receives the same net synaptic weight) and a uniform retinotopic map (displacement of centres of mass of receptive fields in the unoriented layer is strictly proportional to the displacement of the corresponding cells in the oriented layer), we find that imposing a pattern of orientation preference forces the system to violate postsynaptic weight normalization (each cell in the unoriented layer no longer sends forth the same net synaptic weight). We study this deviation from uniformity of the postsynaptic weight, and find that the deviation has a distinct form in the vicinity of the 'pinwheel' singularities of the orientation map. We show that uniform synaptic coverage of the unoriented layer can be restored by introducing a distortion in the retinotopic locations of the receptive fields. We calculate, to first order in the relative elongation of the receptive fields, the retinotopic distortion vector field. Both the pattern of postsynaptic weight non-uniformity and the corrective retinotopic distortion vector field fail to possess the reflection symmetry commonly assumed to relate orientation singularities with topological index $\pm \pi$. Hence, we show that 'right-handed' and 'left-handed' orientation singularities are fundamentally distinct anatomical structures when full 2D synaptic architecture is taken into account. Finally, we predict specific patterns of retinotopic distortion that should obtain in the vicinity of $\pm \pi$ -fold orientation singularities, if uniform pre- and post-synaptic weight constraints are strongly enforced.

Keywords: visual cortex; orientation; retinotopy; fan-in; fan-out; neural network; cortical map.

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1. Introduction

1.1 Anatomy of orientation and position preference in V1

The most prominent feature of mammalian striate cortex (V1) is the spatial organization of response preferences for the position and orientation of elementary visual stimuli (Blasdel & Campbell, 2001; Blasdel & Salama, 1986; Bonhoeffer & Grinvald, 1991; Hubel & Wiesel, 1974). The gross structure of V1 can be approximated as several 2D sheets or layers of cells, distinguished by cell types, sources of input and functional role. Layer IV (of six) receives input from the lateral geniculate nucleus (LGN) of the thalamus, a relay between the retinal ganglion fibres and the cortex. Each thalamic cell is characterized by its receptive field, the region of visual space in which a point stimulus can elicit a response (Kandel et al., 1991). These receptive fields form an orderly, 'topographic' arrangement, with adjacent cells covering overlapping regions of the visual field. The receptive fields of thalamic cells are highly symmetric, being rotationally invariant about their own centres. Moreover, the response of thalamic cells to oriented visual stimuli such as bars or gratings does not show any preference for one direction over another; they are 'unoriented'. In some animals (such as the macaque monkey), the first cells in the visual system to show orientation-tuned responses appear in the 'input layer' (layer IV) of the cortex (Angelucci et al., 2002). In others (such as the ferret), the input layer cells are unoriented and the first oriented cells in the visual pathway occur in layer II/III, which receives synaptic projections from layer IV (Mooser et al., 2004). In the simple geometrical model developed here, we will consider the synaptic projection from an unoriented layer to an oriented layer; the model is intended to apply in both the cases above.

By analogy with thalamic receptive fields, the classical receptive field of a cell in V1 is typically taken to be the region of visual space in which a small bar turned to the optimal orientation elicits a response significantly above the background firing rate. The mechanism of orientation tuning is still debated: one class of models, originating with Hubel & Wiesel (1962), posits that the geometric arrangement of feed-forward synaptic weight from the unoriented to the oriented layer provides the orientation preference. In another class of models, orientation tuning arises from anisotropic lateral connections within the oriented layer (Ben-Yishai *et al.*, 1995; Shouval *et al.*, 2000). Recent experimental evidence has supported the Hubel–Wiesel model: Mooser *et al.* (2001, 2004) demonstrate that the presence of anisotropy in the distribution of axon terminals from unoriented cells in layer IV to orientation-tuned cells in layer II/III of ferret V1 is the principal source of feed-forward orientation bias in this pathway. At the same time, there is evidence that lateral connections within layer II/III of the ferret play a large role in shaping the response to visual stimuli (Chisum *et al.*, 2003).

Receptive fields show a broad range of sizes even at the same point in visual space (Hubel & Wiesel, 1962); at parafoveal eccentricities, e.g. the classical receptive field of a layer IV cell in macaque V1 can range from 0.25° of visual angle (parvocellular pathway) to 1.5° of visual angle (magnocellular pathway) (Angelucci *et al.*, 2002).

The spatial arrangement of orientation preferences features columns spanning the cortical layers in which cells are tuned to similar orientations over a range of roughly 100 μ m laterally (Blasdel, 1992a,b). These columns are arranged around a disordered lattice of orientation preference singularities, about which the orientation preference changes smoothly by $\pm \pi$ (Bonhoeffer & Grinvald, 1991). The overall pattern has an intrinsic spatial scale given by an approximate repeat length, the distance typically separating nearest columns of like orientation preference. This repeat distance is approximately 700 μ m in macaque (Lund *et al.*, 2003; Obermayer & Blasdel, 1993).

As in the thalamus, the map of visual space in V1 is arranged topographically, with a regular procession of the centres of receptive fields through visual field or 'retinotopic' position as position in the

cortex varies (Hubel & Wiesel, 1974). It has been reported that the 'retinotopic map' in the oriented cell layer in cat deviates from a uniformly regular progression at sites that correlate with the locations of the 'pinwheel' singularities in the orientation map, however, this finding remains controversial (Bosking *et al.*, 2002; Buzás *et al.*, 2003; Das & Gilbert, 1997; Hetherington & Swindale, 1999; Yu *et al.*, 2005). Blasdel & Fitzpatrick (1984) observed that in Layer IV of the macaque, cells with more uniformly round receptive fields (similar to the receptive fields of unoriented thalamic cells) also enjoyed a more precise retinotopic arrangement. These results suggest the possibility that the development of orientation preferences might interfere in some manner with maintaining a completely regular retinotopic map.

1.2 Models of orientation and position preference

Models for the formation of cortical maps of orientation and retinotopic position typically suppose a Hebbian or correlation-based mechanism of synaptic plasticity, formulated as a constrained optimization problem. The objective function can reflect the goal of maximizing correlations (Miller, 1994), minimizing an energy function (Durbin & Mitchison, 1990; Goodhill & Willshaw, 1990), minimizing the wiring length required to connect similar and dissimilar columns (Koulakov & Chklovskii, 2001) or 'coverage', the equal representation of all combinations of position, orientation and other features within the cortex (Swindale, 1991).

In a large class of cortical map models, tuning preferences for orientation, retinotopic position and other features of visual stimuli are treated as abstract scalar or vector fields mapped as functions of cortical coordinates $x \in \mathbb{R}^2$ (Durbin & Mitchison, 1990; Goodhill & Willshaw, 1990; Kohonen, 1982; Obermayer *et al.*, 1990; Swindale, 1992; Yu *et al.*, 2005). In another class of model, response preferences arise from the feed-forward architecture of afferent fibres to the cortex (or within the cortex) from an input layer to a 'receiving layer' (Miller *et al.*, 1989). Even though each cortical locus may be assigned to a preferred orientation and retinotopic location (see below), the spread of feed-forward fibres across a local region of the cortex allows for the representation of more than one feature (e.g. orientation) at a given retinotopic location. Indeed, the spread of afferent fibres in cortex is broad enough that the imprecision in the retinotopic map at any point, when transformed via the retinocortical magnification, is roughly equal to the distance that must be traversed to go around a full cycle of orientations (Blasdel & Campbell, 2001; Obermayer & Blasdel, 1993). By mapping these two properties on different scales, it is possible for every combination of 'location' and 'angle' to be represented in cortex.

Classical Hebbian mechanisms, in which correlated firing leads to increased connectivity, generate unstable positive feedback loops that require additional constraining mechanisms (Miller & MacKay, 1994). For example, a model may enforce a hard limit on the total amount of synaptic weight a given postsynaptic cell may receive (Miller *et al.*, 1989). Alternatively, the growth of synaptic weight can be limited by competition for neurotrophic resources (Elliott & Shadbolt, 1998; Harris *et al.*, 1997; Miller, 1998).

Swindale (1991) introduced an optimality principle based on the coverage of the input space by the oriented cortical layer, supposing that it be constrained to represent every combination of orientation, retinotopic position and ocular dominance as uniformly as possible. In this formulation, orientation functions as an abstract label attached to points in the cortex, rather than as a property emerging from an underlying pattern of synaptic weights. By way of analogy, we can consider the 'input' to the representing layer to be the afferent fibres themselves, in which case 'uniform coverage' might be reinterpreted to mean: each presynaptic cell being allotted an equal amount of influence on the activity of the receiving layer. Requiring that each point in the unoriented layer projects the same total feed-forward synaptic weight (or fan-out) to the oriented layer is a natural condition to impose (Goodhill, 1993; Miller *et al.*,

1989), but has not been systematically investigated before in the context of the orientation and retinotopic maps.

This condition of uniform fan-out weight is similar to the requirement that the net weight received by each cell in the cortical layer (the net fan-in weight) be uniform. Miller & MacKay (1994) showed that such uniformity constraints on the net input weights, when applied to a dynamical realization of Hebbian learning, lead to different final weight distributions depending on whether the constraint is enforced multiplicatively or subtractively. Miller further showed that because the constraint surfaces in synaptic weight space corresponding to presynaptic and postsynaptic normalization are not orthogonal to each other, the two constraints can interfere with one another. However, this interference can be controlled by choosing an appropriate set of orthogonal basis directions for subspaces normal to each constraint surface (K. D. Miller, personal communication; see also Miller, 1997).

The model presented here treats orientation and retinotopy as emerging from simple geometrical properties of the feed-forward synaptic weight distribution. The simplicity of our system allows us to examine the architecture of synaptic plasticity constraints governing connections from a 2D 'geniculate' layer to a 2D 'cortex'. Beginning with a system of unoriented receptive fields in the 'cortical' layer, we explore the effects of introducing a perturbation in the form of slightly elongating each receptive field in a direction specified by the nascent orientation preference map. This approach is consistent with experimental results showing that the orientation map emerges gradually, with weak orientation tuning at an early stage of development followed by later sharpening (Chapman & Stryker, 1993). Within our simple geometric model of orientation preference, this perturbation cannot be imposed without violating one of three constraints: uniform pre-synaptic weight, uniform post-synaptic weight and uniform retinotopic mapping. The 2D geometry of feed-forward connections imposes consistency requirements that limit the uniformity of the fan-out or divergence of fibres when the other two constraints are held fixed. In what follows, we show how relaxing the regularity constraint on the retinotopic map allows us to accomodate orientation preference while preserving pre- and post-synaptic weight constraints.

2. Retinotopy and orientation in a feed-forward model

First, we illustrate the interaction of orientation and fan-out given uniform retinotopy. In the simplest feed-forward model, the synaptic weight from a point $r \in \mathbb{R}^2$ in the first layer to a point $x \in \mathbb{R}^2$ in the second layer is given by a non-negative scalar w(x, r). The retinotopic map R(x) corresponding to the centres of the receptive fields of cortical points is given by the 'centre of mass' of the synaptic weights

$$R(x) = \frac{\int_{r} rw(x, r)dr}{\int_{r} w(x, r)dr}.$$
(1)

We denote the net 'fan-in' or 'convergence' to cortical point x by $\lambda(x) = \int_{r \in \mathbb{R}^2} w(x, r) dr$ (see Fig. 1 for illustration). Conversely, the 'fan-out' or 'divergence' from geniculate point r is $\Upsilon(r) = \int_{x \in \mathbb{R}^2} w(x, r) dx$ and the centre of the 'projective field' (Lehky & Sejnowski, 1988) is

$$X(r) = \frac{\int_{x \in \mathbb{R}^2} x w(x, r) \mathrm{d}x}{\gamma(r)}.$$
(2)

As illustrated in Fig. 2, the overlap of the receptive fields of neighbouring cortical points x and x' depends not only on the vector separating those points on the cortical surface, (x - x'), but also on the values of the orientation map $\phi(x)$, $\phi(x')$. Let us suppose each cortical cell has an identical receptive



FIG. 1. Two views of the synaptic weight function w(x, r) (in colour online). **Left:** The fan-in or receptive field is the distribution of synaptic weights afferent to a cortical location x_0 , $w(x_0, r)$. Each of nine output-layer cells (asterisks) is shown receiving 50 contacts from the geniculate layer, with positions drawn from rotationally symmetric Gaussian distributions. **Right:** The fanout or projective field (Lehky & Sejnowski, 1988) is the distribution of synaptic weights efferent from a geniculate location r_0 , $w(x, r_0)$. Each of nine input-layer cells (asterisks) is shown making 50 contacts with the cortical layer, with positions drawn from rotationally symmetric Gaussian distributions.



FIG. 2. Geometric model of feed-forward orientation and retinotopic tuning. The figure illustrates the distribution of feed-forward synaptic weight afferent from cells in the non-oriented layer ('LGN') to two cells in the oriented layer (cortex), labelled **A** and **B**. The overlap of the synaptic weight distributions $w(x_A, r)$, $w(x_B, r)$ is negligible; the distributions could overlap significantly if the orientations or retinotopic locations were varied. Arbitrary units.

field, up to rotation, described by

$$w(x, r|\phi(x)) = G(\mathcal{R}_{-\phi(x)}[x-r]).$$
(3)

Here, $w(x, r|\phi)$ refers to the weight distribution w(x, r) corresponding to a given orientation map $\phi(x)$. $\mathcal{R}_{\phi}[u]$ denotes rotation by ϕ acting on a planar vector u, and the stereotyped receptive field is described by a non-negative function G with total integral one and mean centred at the origin

$$0 \leqslant G(u), \tag{4}$$

$$1 = \int_{u \in \mathbb{R}^2} G(u) \mathrm{d}u,\tag{5}$$

$$0 = \int_{u \in \mathbb{R}^2} G(u) u \, \mathrm{d}u. \tag{6}$$

The overlap between cortical cells at locations x and x', given an overall weight distribution w(x, r), is

$$P(x, x') = \int_{r \in \mathbb{R}^2} w(x, r)w(x', r)dr.$$
(7)

The overlap P(x, x') is not invariant with respect to an arbitrary relabelling of orientation $\phi(x) \rightarrow \phi(x) + \psi$, unless the receptive-field profile G(u) is rotationally invariant. However, the amount of overlap is invariant under a certain rotation operation, namely the transformation

$$\begin{split} \phi(x) &\to \phi(x) + \psi, \\ \phi(x') &\to \phi(x') + \psi, \\ x &\to \mathcal{R}_{\psi} x, \\ r &\to \mathcal{R}_{\psi} r, \end{split}$$

for arbitrary rotations ψ . \mathcal{R}_{ψ} denotes the planar rotation matrix $\begin{pmatrix} \cos(\psi) - \sin(\psi) \\ \sin(\psi) & \cos(\psi) \end{pmatrix}$. This transformation preserves P(x, x') because

$$\begin{split} P(\mathcal{R}_{\psi}x,\mathcal{R}_{\psi}x') &= \int_{r\in\mathbb{R}^2} w(\mathcal{R}_{\psi}x,\mathcal{R}_{\psi}r|\phi(x)+\psi)w(\mathcal{R}_{\psi}x',\mathcal{R}_{\psi}r|\phi(x)+\psi)\mathrm{d}r\\ &= \int_{r\in\mathbb{R}^2} G(\mathcal{R}_{-(\phi(x)+\psi)}[\mathcal{R}_{\psi}(x-r)])G(\mathcal{R}_{-(\phi(x')+\psi)}[\mathcal{R}_{\psi}(x'-r)])\mathrm{d}r\\ &= \int_{r\in\mathbb{R}^2} G(\mathcal{R}_{-(\phi(x)+\psi)+\psi}[x-r])G(\mathcal{R}_{-(\phi(x')+\psi)+\psi}[x'-r])\mathrm{d}r\\ &= \int_{r\in\mathbb{R}^2} G(\mathcal{R}_{-\phi(x)}[x-r])G(\mathcal{R}_{-\phi(x')}[x'-r])\mathrm{d}r\\ &= \int_{r\in\mathbb{R}^2} w(x,r|\phi(x))w(x',r|\phi(x))\mathrm{d}r\\ &= P(x,x'). \end{split}$$

This combined action of rotation on position and angle coordinates is an example of the so-called 'shifttwist' symmetry that plays an important role in cortical pattern formation (Bressloff *et al.*, 2001a,b, 2002; Thomas, 2000; Thomas & Cowan, 2004) as well as computer vision algorithms (Zweck & Williams, 2004). Figure 3 illustrates the shift-twist symmetry that preserves the spatial relationships between a pair of nearby receptive fields.

Figure 4 shows a schematic region of an orientation map with four orientation singularities. Superimposed are ellipses representing oriented receptive fields of cortical points located on a regular grid,

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FIG. 3. Shift-twist symmetry preserves the spatial relationship between adjacent receptive fields (in colour online). The spatial overlap between neighbouring receptive fields is preserved under simultaneous translation (not shown) and by a combined rotation of spatial coordinates and orientation angle. Overlap is not preserved by rotation of spatial coordinates or orientation alone. A: Two receptive fields (retinal coordinates). B: Rotation of the spatial coordinates by $\pi/4$, keeping the orientation angles fixed. C: Rotation of the preferred orientations by $\pi/4$, keeping the retinotopic locations fixed. D: Rotation of both position and orientation by a common angle preserves the alignment, spacing and overlap of the receptive fields.

with each receptive field having a common size and eccentricity. These receptive field profiles are plotted in visual field coordinates under the assumption of an undistorted retinotopic map, $R(x) = x/\mu$, where μ is a constant retinocortical magnification factor converting from degrees of visual angle to cortical millimetres. (For convenience, we will set $\mu = 1$.) The dependence of overlap on the geometry of both orientation and cortical separation is particularly evident near the pinwheels. If we describe the orientations at location θ relative to the centre of a pinwheel as $\phi(\theta) = \pm \theta/2 + \phi_0$, the pattern of overlap will depend both on \pm and on ϕ_0 . In the four-singularity pattern in Fig. 4, the preferred orientation in each quadrant varies around the pinwheel centre as follows:

$$\phi(\theta) = -\theta/2 \phi(\theta) = (+\theta + \pi)/2$$

$$\phi(\theta) = +\theta/2 \phi(\theta) = (-\theta + \pi)/2$$

We can evaluate $\Upsilon(r)$ numerically, given the orientation and retinotopic maps. The shape of the receptive field (see Fig. 2) may be described approximately by its covariance matrix

$$Q(x) = \begin{pmatrix} Q_{11}(x) & Q_{12}(x) \\ Q_{12}(x) & Q_{22}(x) \end{pmatrix}$$
(8)

$$= \frac{1}{\lambda(x)} \int_{r \in \mathbb{R}^2} w(x, r) v v^{\top} dr,$$
(9)



FIG. 4. Left: A pattern of four orientation pinwheels represented by the RGB colour wheel (red = horizontal; green = 120° ; blue = -120° ; see also Fig. 5.). Ellipses (long axis / short axis = 2.0) representing corresponding receptive fields are selected at regular cortical intervals, and plotted in visual-field coordinates. Given undistorted retinotopy, i.e. R(x) = x, the degree of overlap of the receptive fields from neighbouring cortical points varies systematically depending on the orientation map. Note the importance of treating orientation geometrically rather than as an abstract quantity: the variations in overlap would change completely if the orientation map was shifted by a constant angle. **Right:** Projective fields for three points in the lower (LGN) layer. Even though the receptive fields may be richly structured. The top right and lower right projective fields represent the fan-out weight that would be seen upon injection of an anterograde tracer in cells whose retinotopic position corresponded to a point near the top right and lower right orientation singularities, respectively. Note the lack of reflection symmetry relating the projective fields near the upper $(+\pi)$ and lower $(-\pi)$ singularities. (15) and (16) can account for this asymmetry. The centre left projective field reflects the weight projecting from a point corresponding to the centre left of the orientation map, not directly beneath an orientation singularity; nevertheless it is also non-Gaussian in profile.

where $v(x, r) = (r - R(x)) \in \mathbb{R}^2$ is the displacement of *r* from the retinotopic centre of mass R(x), and vv^{\top} is the symmetric 2 × 2 matrix given by the outer product of *v* with itself.

It will be convenient to write Q in terms of its total variance, $\sigma^2(x) = \text{Tr}(Q(x))$, and a traceless symmetric component

$$Q(x) = \frac{1}{2} \{ \sigma^2(x) I_2 + q(x) \Phi_2(\phi(x)) \},$$
(10)

where the scalar fields q(x) and $\phi(x)$ satisfy

$$Q_{11}(x) - Q_{22}(x) = q(x)\cos(2\phi(x)),$$

$$2Q_{12}(x) = q(x)\sin(2\phi(x)).$$
(11)

Here, I_2 is the 2 × 2 identity matrix and $\Phi_2(\phi)$ is the traceless symmetric 2 × 2 matrix that reflects the plane across a line at an angle ϕ

$$\Phi_2(\phi) = \begin{pmatrix} \cos(2\phi) & \sin(2\phi) \\ \sin(2\phi) & -\cos(2\phi) \end{pmatrix}.$$
 (12)

The variance $\sigma^2(x)$ bounds q(x); the latter is strictly positive except when the receptive field afferent to point x is circularly symmetric about R(x), in which case q(x) = 0. For $0 < q(x) < \sigma^2(x)$, the

receptive field is elongated along a direction corresponding to the angle $\phi(x)$. We take $\phi(x)$ to represent a rudimentary preference for orientation, with q(x) representing the strength of the preference. For $q(x) = \sigma^2(x)$, the distribution of afferent weight collapses to a straight line in the input layer.

We henceforth describe receptive fields with the maximum entropy distribution consistent with a given set of zeroth, first and second moments. We assume each cortical locus x has a definite value of fan-in $(\mathcal{A}(x))$, retinotopy (R(x)), width $(\sigma(x))$, orientation preference and tuning strength $(\phi(x), q(x))$, and that these maps are smoothly differentiable save at a finite set of points (e.g. at the singularities in the orientation map). Thus, we take the receptive fields to have the form of ellipsoidal bivariate Gaussians

$$w(x,r) = \frac{\lambda(x)}{2\pi\sqrt{\det Q(x)}} \exp\left[-\frac{1}{2}(r-R(x))^{\top}Q^{-1}(x)(r-R(x))\right],$$
(13)

where det $Q(x) = (\sigma^4(x) - q^2(x))/4$, and the map of preferred orientation $\phi(x)$ enters via the covariance matrix

$$Q^{-1}(x) = \frac{2\sigma^2(x)I_2 - 2q(x)\Phi_2(\phi(x))}{\sigma^4(x) - q^2(x)}.$$
(14)

In what follows we will give examples showing that uniform fan-in and retinotopy $(\lambda(x) = 1; R(x) = x)$ and a non-trivial orientation map $\phi(x)$ with q(x) > 0 naturally give rise to loss of uniformity of the fan-out $\gamma(r)$. We analyse the pattern of fan-out non-uniformity in the vicinity of the positive and negative pinwheel singularities that typically occur in the observed orientation preference maps, and show that the detailed structure of the afferent weights in these two cases fails to exhibit the mirror symmetry that one intuitively expects. Finally, we show that uniform fan-out and uniform fan-in may coexist if one gives up uniform retinotopy, by adding a perturbation $R(x) \rightarrow x + s(x)$. We develop a series expansion for the retinotopic distortion s(x) in terms of a small orientation tuning strength $q \ll 1$, and numerically determine the first-order distortion for some representative orientation maps.

3. Methods

We performed numerical and analytical calculations for two stereotypical orientation map patterns. We used Matlab (The Mathworks) to create multi-dimensional arrays representing the synaptic weights between $N \times N$ grids of input and output layers, assign weights given by specific orientation maps and numerically evaluate the fan-out integrals for these maps. Analytic evaluation of the fan-out integrals was possible near the centre of two types of singularities; the first-order correction to the retinotopic map needed to smooth the fan-out non-uniformity introduced by a given orientation map also was obtained analytically. We set the net fan-in to have unit value for all cortical loci x and fixed the width σ and the tuning strength q to be constant. Using the (presumed small) tuning strength parameter as the scale for our expansion, we set $q = \epsilon$ and introduced a series expansion for the retinotopic distortion vector $s(x) = \epsilon s_1(x) + \epsilon^2 s_2(x) + O(\epsilon^3)$. Analytic expressions were obtained by hand and checked using Mathematica (Wolfram Research). The retinotopic distortion fields given by these calculations were checked numerically by testing the fan-out uniformity of receptive fields created with perturbed retinotopy, again using Matlab. A typical run of the numerical routines took 230 s on a 2.5-GHz G5 running Matlab 7.4 on OS X 10.3.9 Panther (Apple).

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4. Results

4.1 Uniform fan-in, non-uniform fan-out

Having computed w(x, r) numerically for the 100 × 100 sample orientation pattern in Fig. 4, we can compute the projective fields $w(x, r)|_{(r \text{ fixed})}$ and the net fan-out $\Upsilon(r) = \int_{x \in \mathbb{R}^2} w(x, r) dx$. Figure 4



FIG. 5. Left: The net fan-out from each point *r* in the lower (LGN) layer, calculated as the integral over the cortex *x* of the synaptic weight projecting from *r*, for different orientation maps. **Right:** Level curves of the geniculate fan-out superimposed on the map of orientation preference at corresponding cortical loci. The four-singularity pattern in the first and second rows are related by a shift of $\pi/6$ in the orientation at each point. The third row shows a 'roll pattern' representing a single Fourier mode in the orientation map. Parameters: receptive-field width $\sigma = 0.2$ mm; orientation repeat length $\lambda = 0.8$ mm; major to minor axis ratio = 2.0 (strong orientation bias) giving $q/\sigma^2 = 0.6$, or q = 0.024 mm². The entire cortical region shown is 1.6×1.6 mm².

shows three typical projective fields, and Fig. 5 shows the net distribution of fan-out corresponding to the four-singularity pattern. Note that the fan-out and orientation patterns are unchanged by a π -fold rotation. The maximal overrepresentation, i.e. the peak of $\Upsilon(r)$, occurs near but not precisely at the $+\pi$ singularities, while the maximal underrepresentation occurs in the saddle zones between sets of four singularities.

4.2 Asymmetry of $+\pi$ and $-\pi$ pinwheel singularities

Let the orientation tuning strength $q(x) = q_0$, the net fan-in $\lambda(x) = 1$ and the receptive-field width σ be constant in the vicinity of an orientation map singularity at x = 0. Let $(||x||, \theta)$ be the polar coordinate representation of $x \in \mathbb{R}^2$ centred on the singularity, and let the orientation preference map ϕ_{\pm} have the form

$$\phi_{\pm}(\|x\|,\theta) = \pm \frac{\theta}{2} + \phi_0,$$

where '±' indicates a $+\pi$ or $-\pi$ singularity, respectively, and ϕ_0 is an arbitrary offset given by $\phi_{\pm}(||x||, \theta)$ at $\theta = 0$. As ϕ_{\pm} is here assumed to be independent of ||x||, we shall also refer to it as $\phi_{\pm}(\theta)$.

Substituting ϕ_{\pm} into expression (12), we obtain

$$\Phi_2(\theta) = \Phi_2(\phi_0) \cos \theta \mp \Psi_2(\phi_0) \sin \theta,$$

where

$$\Psi_2(\phi) = \begin{pmatrix} \sin(2\phi) & \cos(2\phi) \\ \cos(2\phi) & -\sin(2\phi) \end{pmatrix}.$$

Returning to the expression (13) for the synaptic weights, we obtain

$$w_{\pm}(x,r) = \frac{1}{\pi\sqrt{\sigma^4 - q^2}} \exp\left[-(r-x)^{\top} \left(\frac{\sigma^2 I_2 - q \Phi_2(\phi_{\pm}(\theta))}{\sigma^4 - q^2}\right)(r-x)\right],$$

$$w_{\pm}(x,r) = \frac{1}{\pi\sqrt{\sigma^4 - q^2}} \exp\left[\frac{-1}{\sigma^4 - q^2}(\sigma^2 ||r-x||^2 - q(||x||^2 \cos(2\phi_0 - \theta) - 2||x|| ||r|| \cos(2\phi_0 - \eta) + ||r||^2 \cos(2\phi_0 - 2\eta + \theta)))\right],$$
(15)

$$w_{-}(x,r) = \frac{1}{\pi\sqrt{\sigma^{4} - q^{2}}} \exp\left[\frac{-1}{\sigma^{4} - q^{2}}(\sigma^{2}||r - x||^{2} - q(||x||^{2}\cos(2\phi_{0} - 3\theta) - 2||x|| ||r|| \cos(2\phi_{0} - \eta - 2\theta) + ||r||^{2}\cos(2\phi_{0} - 2\eta - \theta)))\right].$$
(16)

Because the orientation preference map has a singularity at ||x|| = 0, the distribution of synaptic weights afferent to a given postsynaptic location x does not converge to a unique distribution as $||x|| \rightarrow 0$. Approaches along different angles θ approach limiting distributions corresponding to Gaussian ellipses elongated in different directions, corresponding to $\phi_{\pm}(\theta)$. In other words, w(x, r) is not a continuous function of x at the singularity. On the other hand, the distribution of synaptic weights efferent from

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a given presynaptic location r does converge to a definite projective field distribution, i.e. w(x, r) is continuous in r.

It is worth noting that the synaptic weight distributions underlying 'right-handed' and 'left-handed' singularities are not related by a reflection symmetry. In particular, we can compare the projective fields of presynaptic cells located at r = 0, the retinotopic position corresponding to the centre of the orientation map pinwheel in the postsynaptic layer, for both the right- and left-handed cases. The weight distribution efferent from this location is given, respectively, by $w_{\pm}(x, 0)$

$$w_{+}(x,0) = \frac{1}{\pi\sqrt{\sigma^{4} - q^{2}}} \exp\left[-\frac{\|x\|^{2}(\sigma^{2} - q\cos(2\phi_{0} - \theta))}{\sigma^{4} - q^{2}}\right],$$
(17)

$$w_{-}(x,0) = \frac{1}{\pi\sqrt{\sigma^{4} - q^{2}}} \exp\left[-\frac{\|x\|^{2}(\sigma^{2} - q\cos(2\phi_{0} - 3\theta))}{\sigma^{4} - q^{2}}\right].$$
 (18)

The fan-out distribution $\Upsilon_{\pm}(r)$ induced by each singularity can be determined by integrating expressions (15,16) for $w_{\pm}(x, r)$ numerically in the x variable. Figure 6 shows the variation in fan-out near isolated $+\pi$ and $-\pi$ singularities.

4.3 Distorting the retinotopic map can restore fan-out uniformity

The imbalance in fan-out representation can be remedied by shifting the receptive-field centres away from regions of excessive receptive-field overlap, and towards areas of deficient receptive-field overlap. In exchange, the retinotopic map loses its uniform character and develops small distortions on a length scale similar to that of the orientation map. The size of the distortions required to smooth the fanout will depend on the eccentricity of the ellipsoidal profiles of the receptive fields. As the orientation tuning strength $q \rightarrow 0$, the receptive fields become isotropic and the fan-out is uniform with $s \equiv 0$. As a small amount of elongation is introduced, the compensating retinotopic distortion will grow accordingly;



FIG. 6. Distribution of fan-out in the vicinity of (Left) a $+\pi$ orientation singularity and (**Right**) a $-\pi$ orientation singularity (in colour online). Superimposed for reference (in blue) is a sampling of receptive fields on regularly spaced retinotopic centres. Lighter regions reflect larger than average fan-out; darker regions reflect smaller than average fan-out.

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hence, we view the vector field s(x) as depending on the small parameter q. Experimental evidence suggests that the strength of orientation tuning of individual cells does not vary as one moves closer to the pinwheel singularities (Maldonado *et al.*, 1997). We therefore take q to be constant with respect to cortical location x. Subsequently, we will expand s(x) as a series in powers of q.

Taking the fan-out $\Upsilon(r)$ to depend on both the retinotopic distortion vector field s(x) = R(x) - xand the orientation map $\phi(x)$, we write

$$\Upsilon(r|s,\phi) = \int_{x\in\mathbb{R}^2} w(x,r|s(x))dx$$

= $\int_{x\in\mathbb{R}^2} \frac{\lambda(x)}{2\pi\sqrt{\det Q(x)}} \exp\left[-\frac{1}{2}(r-(x+s))^\top Q^{-1}(x)(r-(x+s))\right]dx$
= $\int_{x\in\mathbb{R}^2} \frac{\lambda(x)}{\pi\sqrt{\sigma^4-q^2}} \exp\left[-\frac{(r-(x+s))^\top (\sigma^2 I_2 - q\Phi_2(\phi))(r-(x+s))}{\sigma^4 - q^2}\right]dx.$ (19)

In order to preserve uniform fan-out as q increases from zero, we require the gradient of the fan-out $\nabla_r \Upsilon(r)$ to remain zero, i.e.

$$\nabla_r \Upsilon(r) = -\int_{x \in \mathbb{R}^2} w(x, r|s) \left(-\frac{2}{\sigma^4 - q^2} \cdot (\sigma^2 I_2 - q \Phi_2(\phi))(r - (x + s(x))) \right) dx = 0.$$
(20)

We take the receptive-field width σ to be constant and set the net fan-in $\lambda(x) \equiv 1$. We set $q = \epsilon$ and expand *s* and $\nabla_r \Upsilon(r)$ in powers of ϵ

$$s(x;\epsilon) = \epsilon s_1(x) + \epsilon^2 s_2(x) + \epsilon^3 s_3(x) + \mathcal{O}(\epsilon^4).$$
⁽²¹⁾

Substituting $s(x; \epsilon)$ into (20), we obtain a hierarchy of equations. The terms of zeroth order in ϵ are satisfied automatically because at q = 0 the receptive fields are isotropic

$$0 = \int_{x \in \mathbb{R}^2} (r - x) \exp\left[-\frac{|r - x|^2}{\sigma^2}\right] \mathrm{d}x.$$

The first-order terms in (20) give a convolution equation relating the first-order retinotopic distortion $s_1(x)$ to the orientation preference map $\phi(x)$. Using coordinates u(r, x) = r - x to denote the displacement from the centre of mass (in the unperturbed retinotopy), we have

$$0 = \sigma^2 \int_{x \in \mathbb{R}^2} \exp\left[-\frac{\|u\|^2}{\sigma^2}\right] (\sigma^2 I_2 - 2uu^\top) s_1(x) dx$$

+
$$\int_{x \in \mathbb{R}^2} \exp\left[-\frac{\|u\|^2}{\sigma^2}\right] (\sigma^2 I_2 - uu^\top) \Phi_2(\phi(x)) u \, dx.$$
(22)

This integral equation has the form

$$h(r;\phi) = \int_{u\in\mathbb{R}^2} F(u)s_1(r-u)\mathrm{d}u,\tag{23}$$

where the left-hand side vector $h(r; \phi)$ depends on the orientation map $\phi(x)$. The solution $s_1(x)$ may be formally obtained from the Fourier transforms of the 2 × 2 matrix of convolution kernels *F* and the vector *h*

$$h(r;\phi) = -\int_{u\in\mathbb{R}^2} \exp\left[-\frac{\|u\|^2}{\sigma^2}\right] (\sigma^2 I_2 - uu^{\top}) \Phi_2(\phi(r-u)) u \,\mathrm{d}u,$$
(24)

$$F(u) = \sigma^2 \exp\left[-\frac{\|u\|^2}{\sigma^2}\right] (\sigma^2 I_2 - 2uu^{\top}).$$
⁽²⁵⁾

In order to solve (23) for $s_1(x)$, we assume the orientation map $\phi(x)$ is periodic on a square planar lattice with period 2λ . For the sake of comparison of the roll pattern with the four-singularity pattern, we will take λ to be the period of the rolls or the spacing between adjacent pinwheels, respectively. Denoting the frequency domain vector by k, we take Fourier transforms $\mathcal{F}[\cdot]$ of both sides of (23), obtaining

$$\tilde{F}(k) = \frac{\sigma^{8}}{4} \exp\left[-\frac{\sigma^{2}}{4} \|k\|^{2}\right] kk^{\top},$$

$$\tilde{h}(k) = \frac{-i\sigma^{8}}{16} \exp\left[-\frac{\sigma^{2}}{4} \|k\|^{2}\right] k\beta(k;\phi),$$

$$\beta(k;\phi) = ((k_{1}^{2} - k_{2}^{2})\mathcal{F}[\cos(2\phi(x))] + (2k_{1}k_{2})\mathcal{F}[\sin(2\phi(x))]),$$

$$(kk^{\top}) \tilde{s}_{1}(k) = \frac{-i}{4} k\beta(k;\phi).$$
(26)

As a matrix, (26) is underdetermined; we resolve the ambiguity by choosing the smallest amplitude solution vector \tilde{s} at each frequency k

$$\tilde{s}_1(k) = \frac{-i}{4}k\frac{\beta(k;\phi)}{k^\top k}.$$
(27)

Given an orientation preference map $\phi(t)$ sampled on a cartesian grid, we calculate the discrete Fourier transform of its vector components $\cos(2\phi(x))$, $\sin(2\phi(x))$, apply Formulae (26) and (27), and find a numerical approximation of $s_1(x)$ via the inverse discrete Fourier transform (Matlab, The Mathworks). The first-order correction to the retinotopic vector field obtained for the four-singularity pattern in Fig. 4 is shown in Fig. 7. Applying the first-order term smoothes the fan-out substantially, as shown in Fig. 8.

In order to preserve the smoothest possible feed-forward distribution of fan-out $\Upsilon(r)$ at all points in the input layer, the retinotopic map must be distorted in a specific pattern, particularly in the vicinity of the orientation pinwheels. Figure 7 shows the overall pattern in the vicinity of two pinweels superimposed on the imposed orientation preference pattern. Note the pattern is not symmetric between the right-handed or $+\pi$ (top right and bottom left) and left-handed or $-\pi$ (top left and bottom right) orientation singularities. For the roll pattern, the first-order correction term reduces the deviation of the fan-out more dramatically; the average magnitude of the gradient of the fan-out drops by 90%.

For larger receptive fields ($\sigma \gtrsim \lambda$), the pattern of fan-out non-uniformity appears significantly low-pass filtered in the spatial-frequency domain, and the difference between right- and left-handed singularities diminishes.



FIG. 7. **Top:** The retinotopic distortion vector field s(x) required to smooth the fan-out $\gamma(r)$ after imposition of a four-singularity orientation map. The small arrows represent the vector field, which is smallest in magnitude where the orientation map has a saddle or stationary point, and large near the orientation singularities. RGB colour denotes orientation preference, as indicated. Insets are enlarged below. **Bottom:** Expanded view of retinotopic distortion vector field in the vicinity of a $+\pi$ singularity (**Left**) and a $-\pi$ singularity (**Right**). Note the lack of reflection symmetry between the two vector field insets.

1.02



FIG. 8. Smoothing of the fan-out or postsynaptic weight distribution by applying a first-order shift in retinotopic position. **Top:** the distribution of fan-out with uniform (uncorrected) retinotopy, after an isotropic set of receptive fields is perturbed by imposing an orientation preference map. **Bottom:** the distribution of fan-out after application of the first-order retinotopic shift $s_1(x)$. The left column shows the distribution of net fan-out $\Upsilon(r)$ at different presynaptic (LGN) locations, plotted on a common grayscale axis. Each figure represents a square 280 µm on a side (presynaptic), corresponding to a square region 1.4 mm on a side in the postsynaptic region (presuming a 5:1 magnification factor from LGN to V1). The right column shows a histogram of the fan-out distribution. Applying the retinotopic shift $R(x) = x \rightarrow R(x) = x + qs_1(x)$ reduces the standard deviation of the postsynaptic fan-out by roughly 50%. For the case shown, $\sigma = 0.2$ mm and q = 0.095, $\sigma^2 = 0.0038$ mm², corresponding to a ratio of major to minor receptive field axes of 1.1 (weak orientation bias). The orientation map imposed is the four-singularity pattern shown in the top row of Fig. 5.

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0

5. Discussion

By considering a simple geometrical model of feed-forward orientation tuning, we have shown how three natural constraints on the distribution of synaptic weight interact with one another in the presence of a non-trivial orientation map. Introducing elongated Gaussian receptive fields with uniform fan-in and a uniform retinotopic map induces non-uniformity in the net fan-out projected from different cells in the unoriented or geniculate layer. The fan-out can be smoothed by introducing a compensating distortion of the retinotopic map that shifts receptive-field centres away from regions that are overrepresented in the feed-forward pathway.

The model's simplistic view of orientation tuning is both its greatest strength and its principal drawback. A more complicated model could take into account the structure of input from on- and off-centre geniculate subfields, and the role played by lateral inhibition, anisotropic long-range connections on shaping orientation tuning (Chisum & Fitzpatrick, 2004; Shouval *et al.*, 2000) and anisotropic distribution of feedback connections from V1 to the LGN (Murphy *et al.*, 1999). Further complicating matters, receptive-field size is not an absolute quantity, but depends significantly on contrast and masking effects (Kapadia *et al.*, 1999). However, if we restrict receptive fields to a stereotyped structure (up to rotation), we expect that our main conclusions will not change: a uniform orientation map would yield uniform synaptic coverage; a non-uniform orientation map would introduce fan-out heterogeneities; specific retinotopic distortions could restore a smooth fan-out distribution; the nature of the distortions would be distinct near right- and left-handed orientation singularities. In addition to orientation and visual field location, ocular dominance, or preferential sensitivity to stimuli communicated by one or the other eye, is organized topographically across the cortex. Incorporating some of these additional elements into the model should be straightforward. Imposing a pattern of ocular dominance while maintaining constraints on the net fan-in to the cortex and the net fan-out from separate geniculate layers representing each eye would induce a shift in retinotopy that might provide a natural substrate for processing information about ocular disparity and depth. If similar pre- and post-synaptic weight limits constrain the plasticity of lateral as well as feed-forward weights, we could apply our approach to systems going beyond the Hubel–Wiesel model.

The relative importance of the three constraints considered here is not known; we have assumed that fan-in and fan-out weights provide the strongest constraint on synaptic plasticity. On the other hand, if fan-out weight uniformity and uniform retinotopy were more strictly enforced, then imposing orientation preferences via elongated feed-forward weight distributions would require some cortical populations to receive more net input than others. Such fan-in non-uniformity would vary on a scale similar to the orientation singularities, possibly providing an origin for the cytochrome oxidase 'blob' pattern observed in V1 (Livingstone & Hubel, 1984).

Also unknown is the precise relationship between the key geometric parameters in the model: λ , the length scale governing the spacing of iso orientation patches and pinwheel singularities in V1; σ , the width parameter underlying the spatial reach of afferent inputs and q, the deviation of the input weight distribution from circularly symmetric receptive fields. Angelucci and colleagues (Angelucci et al., 2002; Lund et al., 2003) review several candidate anatomical structures that could underly receptivefield size and orientation tuning in primary visual cortex in Macaque. They report that axons in the magnocellular pathway in the macaque can spread their terminals over a region up to 1.2 mm in diameter. In order to estimate the value of σ in the geometric model corresponding to such a maximal spread, we assume the that receptive field is described by a Guassian distribution and apply order statistics (Hogg & Craig, 1965) to estimate the width parameter σ given the largest observed deviate. Drawing a thousand samples from a circularly symmetric planar Gaussian distribution of width σ (roughly the number of contacts each presynaptic cell makes in the postsynaptic layer), one expects the largest deviate to be roughly 4σ from the centre of the distribution. Hence, a maximum diameter of 1.2 mm would be consistent setting σ in the range 150–300 μ m in the model. Receptive-field widths vary systematically through layer IVC while the orientation map does not. Consequently, there is a range in the value of λ/σ , from 0.25 to 4.0. At the high end of this range (probably typical of the magnocellular pathway in macaque), the fan-out non-uniformity is insignificant and unlikely to play a role in constraining synaptic plasticity, while at the low end (probably typical of the parvocellular pathway) the fan-out nonuniformity is large enough that a constraint mechanism could couple the feature maps as described here. Alternatively, the coupling we predict between orientation and retinotopy might be more pronounced in regions tuned for higher spatial frequency stimuli.

By virtue of its simplicity, our approach allows us to reach surprising and testable conclusions. We find that the deviation from uniform fan-out has a distinct form in the vicinity of pinwheel singularities in the orientation preference map. We show that uniform synaptic coverage of the unoriented layer can be restored by introducing a distortion in the retinotopic locations of the receptive fields. Our geometric

model is simple enough that we can calculate, to first order in the relative elongation of the receptive fields, the retinotopic distortion vector field required to smooth the fan-out distribution.

Surprisingly, we find that both the pattern of post-synaptic weight non-uniformity and the corrective retinotopic distortion vector field fail to possess the reflection symmetry commonly assumed to relate orientation singularities with topological index $\pm \pi$. Most models of cortical map development treat orientation preference as an abstract label rather than an emergent property derivative from an underlying geometric arrangement of synaptic weights. In such abstract models, which include energy-minimization (Durbin & Mitchison, 1990; Goodhill & Cimponeriu, 2000), wire-length minimization (Chklovskii, 2000; Koulakov & Chklovskii, 2001), Kohonen maps (Kohonen, 1982) and centre-surround convolution models (Swindale, 1992), orientation map singularities with topological indices $\pm \pi$ are equivalent up to reflection. Taking into account the 2 × 2 dimensional architecture of feed-forward weights, we show that right-handed and left-handed orientation singularities are distinct anatomical structures. Finally, we predict specific patterns of retinotopic distortion that should obtain in the vicinity of $\pm \pi$ -fold orientation singularities, if uniform pre- and post-synaptic weight constraints are strongly enforced.

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