Ocular dominance patterns in mammalian visual cortex: A wire length minimization approach

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We propose a theory for ocular dominance (OD) patterns in mammalian primary visual cortex. This theory is based on the premise that OD pattern is an adaptation to minimize the length of intra-cortical wiring. Thus we can understand the existing OD patterns by solving a wire length minimization problem. We divide all the neurons into two classes: left-eye dominated and right-eye dominated. We find that segregation of neurons into monocular regions reduces wire length if the number of connections with the neurons of the same class differs from that with the other class. The shape of the regions depends on the relative fraction of neurons in the two classes. If the numbers are close we find that the optimal OD pattern consists of interdigitating stripes. If one class is less numerous than the other, the optimal OD pattern consists of patches of the first class neurons in the sea of the other class neurons. We predict the transition from stripes to patches when the fraction of neurons dominated by the ipsilateral eye is about 40%. This prediction agrees with the data in macaque and Cebus monkeys. This theory can be applied to other binary cortical systems.

I. INTRODUCTION

In the primary visual area (V1) of many mammals, most neurons respond to the stimulation of the two eyes unevenly: they are either left-eye or right-eye dominated. In some species, left-/right-eye dominated neurons are uniformly intermixed in space. In others, left-/right-eye dominated neurons are segregated resulting in a system of alternating monocular regions. This system is known as the ocular dominance (OD) pattern (Wiesel and Hubel, 1974).

Most theorists interested in the OD pattern (Erwin et al., 1993), (Swindale, 1994) have been modeling its development. They succeeded in generating OD patterns of realistic appearance. However, several why rather than how questions remained unanswered. Why, from the functional point of view, do the OD patterns exist? Why do some mammalian species have OD patterns while others do not? Why do monocular regions have different appearances (stripes as opposed to patches) between different species and even between different parts of V1 within the same animal?

Mitchison, 1991, suggested an answer to the first question using the wiring economy principle (Cajal, 1995), (Allman and Kaas, 1974), (Cowey, 1979), (Cherniak, 1992), (Young, 1993), (Chklovskii and Stevens, 1999). The idea is that the evolutionary pressure to keep the brain volume to a minimum requires making the wiring (axons and dendrites) as short as possible, while maintaining function. In general, the function of a cortical circuit specifies the connections between neurons (wiring rules). Therefore the problem presented by the wiring economy principle is to find, for given wiring rules, the spatial layout of neurons that minimizes wire length. Then we can understand the existing layout of neurons as a solution to the wire length minimization problem.

We adopt the wiring economy principle and address the above questions by formulating and solving a wire length minimization problem. Because of the columnar organization of the cortex (Mountcastle, 1957) we consider a two-dimensional neuronal layer of uniform density. The number of the left-eye dominated neurons is a fraction \( f_L \) of the total number, and \( f_R \) is a fraction of right-eye dominated neurons (\( f_L + f_R = 1 \)).

We consider only intra-cortical connections because they constitute the majority of gray matter wiring (LeVay and Gilbert, 1976), (Peters and Payne, 1993), (Ahmed et al., 1994) allowing us to neglect the thalamic afferents and other extra-cortical projections. We assume that each neuron receives synapses from \( N_s \) neurons dominated by the same eye and from \( N_o \) neurons dominated by the opposite eye. In other words, because synapses are unidirectional the resulting wiring rules require each neuron to get unidirectional connections from \( N_s \) neurons dominated by the same eye and from \( N_o \) neurons dominated by the opposite eye.

Given these wiring rules we look for an optimal layout of neurons which minimizes the total length of connections. Depending on the values of \( N_s \), \( N_o \), and \( f_L \), optimal layout belongs to one of the four phases shown in Fig.1 where left-eye dominated neurons are shown in black and right-eye dominated neurons - in white. In the Salt and Pepper phase left-eye and right-eye dominated neurons are uniformly intermixed, Fig.1a. The Stripe phase consists of alternating monocular stripes of neurons dominated by either eye, Fig.1b. The L-Patch consists of the patches of the left-eye dominated neurons surrounded by the right-eye dominated neurons, Fig.1c. The R-Patch consists of the patches of the right-eye dominated neurons surrounded by the left-eye dominated neurons, Fig.1d.

Our approach differs from Mitchison’s in that we drop
the retinotopy requirement, that is our wiring rules do
not take into account receptive field positions. This
simplification is supported by the existence of the receptive
field scatter (Hubel and Wiesel, 1974), random variation
in the receptive field position between adjacent neurons.
For example, in a macaque retinotopy exists only on the
scales greater than \( \approx 1 \) mm (Hubel and Wiesel, 1974),
which exceeds the typical size of monocular regions. By
disentangling the retinotopy from the OD problem we
simplify it enough to map out a phase diagram.

In the Discussion we compare our predictions with
the data from macaque and Cebus monkeys and find
good agreement. Also, we discuss simplifying assump-
tions made in the paper and possible ways to extend the
theory.

![FIG. 1. Different appearances of the ocular dominance pa-
ttern. Left-eye dominated neurons are white while right-eye
dominated neurons are white.(a) Salt and Pepper phase, uni-
formly intermixed left/right neurons.(b) Stripe phase, alter-
nating monocular stripes.(c) L-Patch phase, circular left-eye
islands in the right-eye sea. (d) R-Patch phase, circular right-
eye islands in the left-eye sea.](image)

**II. RESULTS**

We present the central results of the paper on a phase
diagram, Fig. 2, showing optimal phases for various ratios
of same-eye to other-eye connections \( N_s/N_o \) and fractions
of left-eye neurons \( f_L \). If the numbers of same-eye and
other-eye connections are equal, \( N_s/N_o = 1 \) then Salt
and pepper is optimal. Otherwise, if \( N_s/N_o \neq 1 \)
the wirelength is minimized by an OD pattern consist-
ing of alternating monocular regions. The shape of these
regions depends on the relative fraction of the left-eye
dominated neurons, \( f_L \). When the numbers of neurons
dominated by each eye are close, \( f_L \approx f_R \), the Strip-
ate phase is optimal. When the fraction of left-eye (right-eye)
dominated neurons drops below a critical value \( f_c \approx 0.4 \nthe L-Patch (R-Patch) phase becomes optimal. Our pre-
dictions of the critical value agree with the data from
macaque and Cebus monkeys.

![FIG. 2. Ocular dominance phase diagram calculated in the
lattice model. Optimal phases are shown as a function of
the relative number of the same-eye to other-eye connections
\( N_s/N_o \) and a fraction of left-eye neurons \( f \). Range of the
Stripe phase optimality is shown in black, Patch phase - in
white, Salt and Pepper - in grey.](image)

In the following section we formulat a wiring problem
on a lattice. For small \( N_s \) and \( N_o \) we solve it analyti-
while for large \( N_s \) and \( N_o \) we solve it numerically. Results
are shown in Fig. 2. Next, we introduce a continuous for-
mulation of the problem. We prove that Salt and Pepper
is an optimal layout when \( N_s = N_o \). Then we show that
for \( N_s \neq N_o \) segregation of neurons according to their
OD reduces wire length. We calculate in perturbation
theory the wire length for Stripe and Patch phases and
find the range of parameters for the optimality of each
phase. Perturbation theory provides an analytical treat-
ment of neuronal clustering so common throughout the
nervous system. The calculated phase diagram is similar
to that obtained in the lattice model.

**A. Lattice model**

Although the arrangement of neurons in cerebral cor-
tex is anything but grid-like we can understand many fea-
tures of the neuronal layout by studying lattice models.
These models compensate in clarity and computability
what they lack in realism. Of course, we need to make
sure that the results are independent of the particular
choices of lattice parameters (for example the number of
nearest neighbors).

We consider arranging a large number of neurons on
a two-dimensional square lattice. Each site must be oc-
cupied by either left-eye or right-eye dominated neuron.
The number of the left-eye dominated neurons is a frac-
tion \( f_L \) of the total number of neurons and \( f_R \) is a frac-
tion of right-eye dominated neurons. The problem is to
find a layout which minimizes the total length of wiring specified by the following rule. Each left-eye neuron has unidirectional connections with $N_l$ left-eye neurons and with $N_o$ right-eye neurons. Each right-eye neuron has unidirectional connections with $N_s$ right-eye neurons and with $N_o$ left-eye neurons. Unidirectionality of connections means that connecting neuron A to neuron B, does not necessarily imply that neuron B connects to neuron A. The motivation for this rule comes from the unidirectional properties of synapses in the brain.

Because we attempt to minimize wire length we assume that for a given layout the connections are established optimally. Thus the problem is reduced to comparing optimal wiring for various layouts. Therefore, we will assume that each neuron makes the shortest possible connections satisfying wiring rules.

**Small numbers of connections per neuron.** We start by finding optimal layouts for three illustrative examples of wiring rules with small numbers of connections, $N_s$ and $N_o$. We caution the reader that because of the small numbers of connections phase assignments may seem arbitrary. These examples are chosen to illustrate our main results which will be confirmed both in the lattice model with large $N_s$ and $N_o$ later in this section and in the continuous model (section IIB).

For the first two examples we set equal numbers of left and right neurons, $f_L = f_R = 1/2$. In the first example each neuron connects with equal numbers of the same-eye and other-eye neurons, $N_s = N_o = 2$. Then the optimal layout is the system of alternating rows of left/right neurons, Fig. 3a. This layout is a realization of the Salt and Pepper phase, Fig. 4a, because each neuron has an equal number of left and right neurons among its nearest neighbors. To calculate the length of connections per neuron, $l$, we notice that in this layout all neurons have the same pattern of connections. By considering one of them, Fig. 3a, we find that $l = 4$. This layout is optimal because each neuron makes all of its connections with nearest neighbors.

For the second example each neuron connects with more same-eye than other-eye neurons: $N_s = 3, N_o = 1$. Then a realization of the Salt and Pepper phase, Fig. 4b, is not optimal anymore. The length of connections per neuron is $l ≈ 4.41$, while the Stripe phase, Fig. 5b, gives $l = 4$. The Salt and Pepper phase loses in wiring efficiency because there are not enough same-eye neurons among nearest neighbors and connections with the next nearest neighbors are needed. The Stripe phase, Fig. 5b, rectifies this inefficiency by having each neuron make connections only with nearest neighbors. Thus, clustering of same-eye neurons is advantageous if each neuron connects more with the same-eye than with the other-eye neurons.

A suboptimal layout for the same wiring rules is illustrated by a realization of the Stripe phase, Fig. 3b. In this layout each neuron has the same pattern of connections up to a mirror reflection. By considering one of them, Fig. 5b, we find $l = 3 + \sqrt{2} ≈ 4.41$, greater than $l = 4$ for the Salt and Pepper phase. Here each neuron has among its nearest neighbors only one other-eye neuron, while the wiring rules require connecting with two other-eye neurons. A connection to the next nearest neighbor is longer making the layout suboptimal. We confirm the optimality of the Salt and Pepper phase for $N_s = N_o$ both numerically for large $N_s$, $N_o$ and analytically.

In the second example each neuron connects with more same-eye than other-eye neurons: $N_s = 3, N_o = 1$. Then a realization of the Salt and Pepper phase, Fig. 4b, is not optimal anymore. The length of connections per neuron is $l ≈ 4.41$, while the Stripe phase, Fig. 5b, gives $l = 4$. The Salt and Pepper phase loses in wiring efficiency because there are not enough same-eye neurons among nearest neighbors and connections with the next nearest neighbors are needed. The Stripe phase, Fig. 5b, rectifies this inefficiency by having each neuron make connections only with nearest neighbors. Thus, clustering of same-eye neurons is advantageous if each neuron connects more with the same-eye than with the other-eye neurons.
B. Continuous model

In these layouts, different neurons have different patterns of connections. To find the wiring length per neuron we average over different patterns and find for the Salt and Pepper phase $l \approx 5.02$ and for the Stripe phase $l = 4.5$. A more efficient layout is the L-Patch phase, Fig. 4, where $l \approx 4.21$. Although we cannot prove that the L-Patch phase is optimal, this seems likely. Thus, the optimal shape of monocular regions depends on the relative numbers of left/right neurons.

Large numbers of connections per neuron. Lattice models with small numbers of connections per neuron yield quick results good for illustration purposes. However, they are difficult to generalize to the wiring rules with large numbers of connections more appropriate for cortical circuits where each neuron connects with $\approx 10^4$ neurons. For example, attributing the layouts in Fig. 3 to the Salt and Pepper phase rather than the Stripe phase may seem arbitrary. Therefore we study lattice problems with large numbers of connections per neuron.

When the number of connections per neuron is much greater than the number of nearest neighbors, the effect of the discreteness of the lattice on the results is negligible. In particular, for a given fraction $f_L$ and ratio $N_s/N_o$ only the periodicity of the optimal layout depends on the $N_o$. Thus the solution of the wire length minimization problem for one value of $N_o$ can be generalized to other problems with the same $f_L$ and $N_s/N_o$.

We solve the wire length minimization problem using the following numerical algorithm. We fix the values of $f_L$ and $N_s/N_o$. We consider neuronal layouts belonging to several phases: Salt and Pepper, Stripe, L-(R-)Patch (both triangular and square lattice), Checkerboard (only for $f_L = 1/2$). For each phase we find the optimal period which minimizes wirelength. Then we compare wire length in the optimal layouts of different phases. We plot the optimal phases for various values of $f_L$ and $N_s/N_o$ on the phase diagram, Fig. 4. These results were discussed above.

- Satisfy the wiring rules ($N_s$ same and $N_o$ other neuron connection have to be established);
- Minimize the total wire length.

In the end of the subsection we calculate the wire length for the Salt and Pepper configuration.

We consider the mixture of neurons of two types: dominated by the left and right eyes. We assume that the neurons are located in the plane. This assumption is based on the fact that the OD remains constant in the direction perpendicular to the cortex surface. The variables of the problem can therefore be considered functions of the remaining two coordinates, $r$.

Instead of considering each individual cell we characterize the neuron configuration by continuous local variables. We define the local density of neurons dominated by the right eye $n_R(r)$ as the average density in a square containing sufficiently large number of cells ($> 10$), yet small compared to the typical spatial scales of the configuration ($\sim 1\text{mm}$). Similarly $n_L(r)$ is the local density of cells dominant by the left eye. Although both $n_R(r)$ and $n_L(r)$ can vary in space, the total density of neurons

$$ n_o = n_R(r) + n_L(r) $$

is a constant, independent of the position in the cortex.

In our model $n_R(r)$ and $n_L(r)$ completely define the neuron configuration. For example the Salt and Pepper configuration, in which the densities of right-eye and left-eye neurons are uniform, can be defined as follows

$$
\begin{align*}
n_R(r) &\equiv \bar{n}_R = f_R n_0, \\
n_L(r) &\equiv \bar{n}_L = f_L n_0, \\
\bar{n}_R + \bar{n}_L &= n_0,
\end{align*}
$$

Here $f_R$ is defined as the fraction of the right-eye neurons with respect to the total number of cells (in general not 1/2).

Having defined the neuron configuration by fixing the densities $n_R(r)$ and $n_L(r)$ we proceed to establishing the connections between cells. Two requirements have to be taken into account. First, we have to satisfy the wiring rules. Second, for given densities $n_R(r)$ and $n_L(r)$ the total length of connections has to be minimum. Consider a pattern of connections from a neuron dominated, for example, by the right eye. Consider also the region in the cortex it is connected to. There are in fact two such regions, for the right- and left-eye connections. We claim that each of these regions is a disc. To prove this, notice that if the connections are produced with neurons outside of this disk rather than inside the wire length is increased. This is inconsistent with the requirement of the optimum wiring for a given configuration. We denote the radii of these two disks $R_{RR}(r)$ and $R_{RL}(r)$, implying the radii of right-eye neuron at point $r$ connection regions.
to the right-eye and left-eye cells correspondingly. Similar quantities can be introduced for the left-eye neurons at point $r$, i.e., $R_{L,R}(r)$ and $R_{L,L}(r)$. We introduce the index notation $i = \{R, L\}$. Then the four radii discussed can be collapsed into one notation $R_{ik}(r)$, standing for the radius of the connection region for the neuron of OD $i$ at point $r$ to the cells of OD $k$. The radius can be determined from the wiring rules ($N_s$ and $N_o$ connections to the cells of the same and other OD respectively have to be established):

$$N_{ik} = \int_{|r - r'| \leq R_{ik}(r)} dr' n_k(r').$$  \tag{2}

Here the elements of matrix $N_{ik}$, $i = \{R, L\}$ are equal to $N_s$ if $i = k$ and $N_o$ otherwise.

It is now possible to determine the total connection length in the cortex $\mathcal{L}$. To this end we add up the lengths of the connections of individual neurons $L_{ik}(r)$ over the whole area:

$$\mathcal{L} = \int dr n_i(r) \sum_{i,k = R,L} L_{ik}(r),$$ \tag{3}

where

$$L_{ik}(r) = \int_{|r - r'| \leq R_{ik}(r)} dr' n_k(r') |r - r'|.$$ \tag{4}

The last factor in this expression is the connection length as a function of separation $r - r'$ between neurons. In principle, cost function may not be a linear function of separation. However, we take it to be linear for the sake of simplicity. Eqs. (2) - (4) define our model completely.

Using Eq. (3) we calculate the wire length for the homogeneous Salt and Pepper configuration. To this end we substitute the densities given by Eq. (1) into (2) to find:

$$R_{SP}^{ik} = \sqrt{\frac{N_{ik}}{\pi n_k}}.$$ \tag{5}

Then using Eqs. (3) and (4) we obtain

$$L_{ik} = \frac{2}{3} R_{SP}^{ik}$$ \tag{6}

and finally

$$L_{SP} = \frac{2A}{3} \left[ \sqrt{\frac{N_I^2}{\pi}} (\sqrt{n_R} + \sqrt{n_L}) + \sqrt{\frac{N_o^2}{\pi}} \left( \frac{n_R}{\sqrt{n_L}} + \frac{n_L}{\sqrt{n_R}} \right) \right],$$ \tag{7}

where $A$ is the total area of the cortex.

In the next subsection we show that wire length can be reduced with respect to (6) by introducing a small inhomogeneity into the neuron densities $n_R$ and $n_L$. To this end we treat our model (3) - (4) in the framework of the perturbation theory.

**Instability of the Uniform State Leads to the Formation of Patterns.** The purpose of this subsection is to study structures that do not deviate far from the uniform Salt and Pepper configuration discussed in the previous subsection. Because we have solved the uniform configuration exactly, the configurations which are not far from it are also treatable by the perturbation theory analysis i.e., expansion of the wire length (3) in terms of the deviation of densities of right and left-eye neurons from the constant. This treatment determines which of the inhomogeneous phases (Stripe or Patch) is optimum. Also, comparison with the numerical results shows that the perturbation theory results hold even for big differences in density.

We therefore consider a small repositioning of neurons, leading to the deviation of densities from constant $\delta n(r)$. Because $n_R + n_L = n_0$

$$n_R(r) = \bar{n}_R + \delta n(r),$$

$$n_L(r) = \bar{n}_L - \delta n(r).$$ \tag{8}

As this is only rearrangement the average of $\delta n(r)$ over the entire volume $\bar{n}_n(r)$ is zero, i.e., the total number of left and right eye neurons is not changed by the perturbation. We then substitute these functions into our model (3) - (4) and calculate expansion of the wire length in the Taylor series in $\delta n(r)$. It has the form:

$$\mathcal{L} = \mathcal{L}^{SP} + \mathcal{L}^{(1)} + \mathcal{L}^{(2)} + \ldots,$$ \tag{9}

where $\mathcal{L}^{SP}$ is given by Eq. (7), $\mathcal{L}^{(1)} \propto \delta n$, $\mathcal{L}^{(2)} \propto \delta n^2$ are the first and the second order corrections to the wire length. From the condition $\delta n(r) = 0$ it follows that $\mathcal{L}^{(1)} = 0$. The second order correction to the wire length is

$$\mathcal{L}^{(2)} = \int dr dr' \sum_{i,k = R,L} R_{SP}^{ik}$$

$$\times \left\{ U_{1ik}(r - r') \delta n_i(r) \delta n_k(r') + U_{2ik}(r - r') \delta n_k(r) \delta n_k(r') \right\}.$$ \tag{10}

Here $\delta n_i(r)$ is the perturbation of density of neurons of $i$-th dominance ($\delta n_R = \delta n$, $\delta n_L = -\delta n$) and

$$U_{1ik}(r) = \theta \left( R_{SP}^{ik} - |r| \right) \left( \frac{|r|}{R_{SP}^{ik}} - 1 \right),$$ \tag{11}

$$U_{2ik}(r) = \frac{1}{4\pi (R_{SP}^{ik})^2}$$

$$\times \int dr'' \theta \left( R_{SP}^{ik} - |r - r''| \right) \theta \left( R_{SP}^{ik} - |r''| \right),$$ \tag{12}
where \( \theta(x) = 1 \), if \( x \geq 0 \), and \( \theta(x) = 0 \), if \( x < 0 \). Because \( U_{2ik} \) has the geometrical interpretation of the overlap between two disks:

\[
U_{2ik}(r) = \left[ \frac{1}{2\pi} \arccos\left( \frac{|r|}{2R_{ik}^{\text{SP}}} \right) - \frac{|r|}{4\pi R_{ik}^{\text{SP}}} \right] \theta\left(2R_{ik}^{\text{SP}} - |r|\right). 
\]

Using Eq. (8) we express the second order correction to the wire length (10) as a pairwise density-density interaction

\[
\mathcal{L}^{(2)} = \int \! dr \! dr' \delta n(r) \mathcal{U}(r - r') \delta n(r'), \quad (14)
\]

where the “interaction potential” \( \mathcal{U}(r) \) is given by

\[
\mathcal{U}(r) = \mathcal{U}_1(r) + \mathcal{U}_2(r),
\]

\[
\mathcal{U}_1 = U_{1RR} + U_{1LL} - U_{1RL} - U_{1LR},
\]

\[
\mathcal{U}_2 = U_{2RR} + U_{2LL} + U_{2RL} + U_{2LR}.
\]

We therefore analyze the conditions at which the function has negative values. Two statements can be made in this respect. First, assume that \( N_s = N_o \). Then \( \mathcal{U}(q) \) is never negative. This implies that Salt and Pepper is optimum if \( N_s = N_o \). Second, consider \( \mathcal{U}(q) \) at \( f_r = f_L = 1/2 \) and arbitrary \( N_s \neq N_o \). In this case \( \mathcal{U}(q) \) always has negative values. This means that on the line of equal right-left eye occupancy \( f_r = f_L = 1/2 \) the OD patterns are always optimum, except for the point \( N_s = N_o \). We do not give the proofs of these properties due to the space limitations.

![FIG. 6. Function \( \tilde{U}(q) \) calculated numerically for \( N_s = 10, N_o = 7, f_r = 1/2, \) and \( n_0 = 1 \). The value of wave vector corresponding to the most negative value of the function is denoted \( Q_0 \).](image)

To illustrate these properties we show an example of \( \tilde{U}(q) \) in Fig. 6. The function obviously has negative values, signifying instability and an OD pattern formation. The instability is strongest at the wave vector corresponding to the most negative value of \( \tilde{U}(q) \). Indeed, creating the structure at this wave vector reduces the total wire length most effectively. We predict therefore the spatial period of the OD pattern. For the case \( N_s \approx N_o \) shown in Fig. 6 (\( N_s = 10 \) and \( N_o = 9 \)) function \( \tilde{U}(q) \) reaches the most negative value at

\[
Q_0 \approx 3 \frac{R_{RR}^{\text{SP}}}{R_{RL}^{\text{SP}}} \approx 3 \frac{R_{RL}^{\text{SP}}}{R_{LR}^{\text{SP}}},
\]

The spatial period of the OD pattern is therefore

\[
\Lambda = 2\pi Q_0 \approx 2R_{RR}^{\text{SP}} \approx 2R_{RL}^{\text{SP}}.
\]
In other words it is approximately equal to the diameter of the disc of connections.

**Competition between the Stripe and Patch phases** Next we use the perturbation theory to calculate approximately the wire lengths of different OD structures. Because the structures are periodic the integral in Eq. (18) can be reduced to the sum over the reciprocal lattice vectors $Q$:

$$
\mathcal{L}^{(2)} = \frac{1}{A} \sum_{Q \neq 0} \tilde{U}(Q) |\delta n(Q)|^2,
$$

where $A$ is the total area of the system. Different OD structures have different sets of $Q$ and $\delta n(Q)$. For example, for **Strips** $Q_x = 2\pi n/\Lambda$, $Q_y = 0$, where $n = \pm 1, \pm 2, \ldots$ and $\Lambda$ is the spatial period of the structure. The Fourier transform of density

$$
\delta n_{\text{Strips}}(Q) = \frac{2A}{\Lambda |Q|} \sin \left( \frac{f_R |Q| \Lambda}{2} \right).
$$

For the triangular lattice of **Patches** $Q_x = Q_0(l\sqrt{3}/2)$, $Q_y = Q_0(k + l/2)$, with $l, k = \pm 1, \pm 2, \ldots$ and $Q_0 = 4\pi/\Lambda \sqrt{3}$, where $\Lambda$ is the lattice spacing. The Fourier transform of density

$$
\delta n_{\text{Patches}}(Q) = \frac{2A}{\Lambda |Q|} \sqrt{\frac{2\pi f_R}{\sqrt{3}}} \sin \left( Q|\Lambda| \sqrt{\frac{f_R \sqrt{3}}{2\pi}} \right).
$$

Based on Eqs. (21)-(23) we compare different OD structures and generate the phase diagram similar to one given in the introduction (see Fig. 7).

**FIG. 7.** Ocular dominance phase diagram calculated in perturbation theory. Range of the **Stripe** phase optimality is shown in black, **Patch** phase - in white, **Salt and Pepper** - in grey.

Figures 2 and 7 have many similar features. First, the diagram is symmetric with respect to the line $f_R = 1/2$. This is a consequence of the left-right eye symmetry of the general wire length functional (3) inherited by the second order functional (18). The reason for the existence of such a symmetry is interchangeability of left and right eyes inherent to this model. If, for instance, in a given configuration one relabels left-eye neurons into the right-eye ones and vice versa, the wire length does not change.

Second, the **Salt and Pepper** phase occupies a stripe around the line $N_s = N_o$. The width of this line is given by $|N_s - N_o| < 0.01 N_o$. This is the result of the above-mentioned stability of **Salt and Pepper** on the line $N_s = N_o$. As it is shown by the diagram the stability extends into some region around this line.

Third, there is a transition between **Strips** and **Patches** at $f_R \approx 0.4$ and 0.6. The region on the diagram corresponding to $0.4 < f_R < 0.6$ is almost completely occupied by the **Strips** while the rest of the diagram ($f_R < 0.4$ and $f_R > 0.6$) by the **Patches**. We explain this in the framework of the perturbation theory. The main contribution to Eq. (21) comes from the terms with the smallest $|Q|$. This happens because both $\tilde{U}(Q)$ and $\delta n(Q)$ decay very fast with the increase of $|Q|$. **Strips** and **Patches** can approximately be compared using only the terms with the smallest $|Q| \equiv Q_0$. The two solutions have equal wire length if

$$
2\tilde{U}(Q_0) |\delta n_{\text{Strips}}(Q_0)|^2 = 6\tilde{U}(Q_0) |\delta n_{\text{Patches}}(Q_0)|^2,
$$

where the factors 2 and 6 are the numbers of the smallest wave length harmonics in the **Stripe** and **Patch** phases respectively. Using Eqs. (22) and (23) to solve the latter equation for $f_R$ we obtain numerically for the filling factor of the transition $f_R \approx 0.4$. Due to the mentioned left-right eye symmetry of the model similar transition occurs at $f_R = 1 - 0.4 = 0.6$.

We would like to notice finally that comparison of the perturbation theory to exact calculations shows that the former works well even if the deviation of the density from constant is not small ($\sim 0.5 n_0$). Such a comparison shows that $(1 - \mathcal{L} - \mathcal{L}^{\text{SP}}) / \mathcal{L}^{(2)} < 5\%$. In addition the perturbation theory provides a framework to understand numerous qualitative features of the phase diagram discussed above.

Von der Malsburg, 1979, has surmised that there is a phase transition between **Patches** and **Strips** driven by the cost of the left/right eye boundary. However he did not address different numbers of connections with same vs. other-eye neurons and made several different assumptions (e.g. fixing the periodicity of the pattern). Thus our results offer a more complete description of the OD patterns while relying only on one principle - wire length minimization.
### III. DISCUSSION

#### A. Comparison with experiment

This theory relates functional requirements on a neural circuit to its structural properties. In particular, the phase diagram relates the relative fractions of neurons, \( f_L \), and of connections, \( N_s/N_o \), to the appearance of the OD pattern. Ideally, this theory could be tested by measuring these numbers experimentally and comparing the observed OD pattern to the one predicted by the phase diagram. However, we could not find data on the ratio \( N_s/N_o \) and can only surmise that it is greater than one.

We can partially test the theory by using the predictions of the phase diagram which are independent of the ratio \( N_s/N_o \). Fig. 8 shows that the transition from the Stripe and the L-Patch (R-Patch) phase takes place when \( f_L \approx 0.4 \) (\( f_R \approx 0.4 \)) for a wide range of \( N_s/N_o \). This number can be compared with the experimentally derived value of \( f_L \) which is found from the relative area occupied by left-eye dominated neurons. The prediction that the Patch phase becomes optimal when one eye dominates is, indeed, non-trivial because there may be a system of alternating wide and narrow monocular stripes instead.

We test this prediction on the data from macaque and *Cebus* monkey. The relative area occupied by the left/right eye depends on the location in V1. In parfoveal part of V1 both eyes are represented equally, \( f_R \approx 0.5 \). In agreement with the phase diagram, the OD pattern consists of stripes. Farther from the fovea contralateral eye becomes dominant. The OD pattern becomes patchy there, just as expected from the phase diagram. We verify the location of the transition by using the following algorithm. We find \( f_L \) for each point of the pattern by calculating the relative area occupied by the left/right regions in a window centered on that point and a few OD periods wide (dashed lines in Fig. 8). Then we draw a contour corresponding to \( f_L = 0.4 \), Fig. 8. Next we check visually whether the location of this contour is close to the transition from Stripes to Patches. Indeed, the large black contour in Fig. 8 coincides with the transition indicating good agreement.

In *Cebus* monkey the OD pattern has a similar transition (Rosa et al., 1992). For monkey CO6L from Rosa et al., 1992, we determine visually that along the horizontal meridian the transition occurs at the eccentricity of 20 – 40 degrees. According to the plot of the relative representations given in Rosa et al., 1992, \( f_L \) changes in the range 0.32 – 0.42 at these eccentricities. Our prediction of \( f_R = 0.4 \) falls into this interval. For the upper 45 degree meridian of the same monkey the transition occurs at the eccentricity of 30 – 40 degrees or at filling fractions 0.33 – 0.43. Again, the predicted value belongs to this interval. We conclude that this data agrees with our predictions although a more precise measurement would be helpful.

In cats the OD patterns resemble Patches. In this case our theory implies that one eye should dominate. In fact, Shatz and Stryker, 1978, reported that the filling fraction of the contralateral eye in cat V1 is greater than 0.5. This may explain the existence of Patches in cat V1. However, other authors (Anderson et al., 1988) claimed that both eyes are represented almost equally. More precise measurements of the ocular dominance are needed to make a conclusive judgment.

![Transition between the Stripe and Patch phases](image)

**FIG. 8.** Transition between the Stripe and Patch phases occurs at theoretically predicted value \( f_L \). Shown is a fragment of the macaque ocular dominance pattern from Horton and Hocking, 1996. Neurons dominated by the left eye are grey and neurons dominated by the right eye are white. Black contours correspond to the value \( f_L = 0.4 \) averaged over a window equal to the one shown (dashed lines). Transition from Stripe to Patch phase visually coincides with the black contour.

#### B. Further Development of the Theory

Next, we elaborate on several simplifying assumptions made in the paper. Although these assumptions should not affect our conclusions significantly, they are worth further exploration.

First, the transition between Stripes and Patches may be more complex than discussed. We considered only two candidate phases: Stripes and a triangular lattice of circular Patches. It is possible that some intermediate phases become optimal near the transition. For example, Fig. 8 hints that parallel chains of elongated Patches may give more efficient wiring. This would slightly modify our phase diagram.

Second, we based our theory on looking for an optimal layout of neurons which minimizes total wire length.
The considered structures are, therefore, regular and periodic. However, developmental noise may lead to fluctuations in the OD pattern which reduce slightly its wiring efficiency. Although actual OD patterns contain such fluctuations we do not know whether these are due to suboptimal wiring or variations in the wiring rules from point to point.

Different phases may have different stability in respect to noise. Judging from the data, the Stripe phase holds up well on the scale of a few periods. The Patch phase, however, does not show a regular triangular lattice. We think that this is because of a relatively small difference in wire length between the triangular and the square lattice of Patches. (It is about 0.5% of the total wire length, compared to 2% difference between Stripes and Patches for the upper left part of the phase diagram.)

Third, we ignored the presence of numerous other cortical maps, such as orientation selectivity and retinotopy of receptive fields. This follows from the assumption that the mutual interaction (or coupling) between different maps is weak. For example, as mentioned in the Introduction, our motivation to neglect retinotopy comes from the magnitude of the receptive field scatter exceeding the width of ocular dominance stripes. The best justification for ignoring the coupling between the maps comes from the robustness of the observed OD patterns and the good agreement of our theory with experiment.

Our theory can be expanded to address the interaction between different maps. Variables of other maps can enter the expression for the total wire length, Eq.3, through additional values of indices $i$ and $k$, which so far reflect ocular dominance. Moreover, these indices can become continuous variables if the sums (3) are replaced by integrals. This would be appropriate for including interactions with retinotopic and orientational selectivity maps.

Fourth, we applied our theory to the OD patterns as the best studied structure. Since our model is based on minimal assumptions, it can be applied to other binary structures such as cytochrome oxidase blobs.

In conclusion, we explained the OD patterns in mammalian V1 by minimizing wire length given general functional considerations. Good agreement with experiment lends strong support to the notion that OD structures are adaptations to reduce intra-cortical wiring.

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