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EU ADVANCED COURSE IN COMPUTATIONAL NEUROSCIENCE

An IBRO Neuroscience School

(30 July - 24 August 2001)

"Hallucinations/Long-Range Connections"

presented by:

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These are preliminary lecture notes, intended only for distribution to participants.

Mathematical theory of primary visual cortex: from geometric hallucinations to contextual effects

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Visual hallucinations

... the hallucination is ... not a static process but a dynamic process, the instability of which reflects an instability in its conditions of origin

R. MOURGUE (1932)

- Various sources of hallucinations:

  exposure to flickering lights (Purkinje, Helmholtz)

  administration of certain anaesthetics

  waking up or falling asleep

  deep binocular pressure on the eyeballs

  the ingesting of drugs

- In 1928 Klüver classified various reported images into four classes or *form constants*:

  tunnels and funnels (I)

  spirals (II)

  lattices such as honeycombs (III)

  cobwebs (IV)

Hypothesis I: Geometric visual hallucinations are generated *ab initio* in V1.

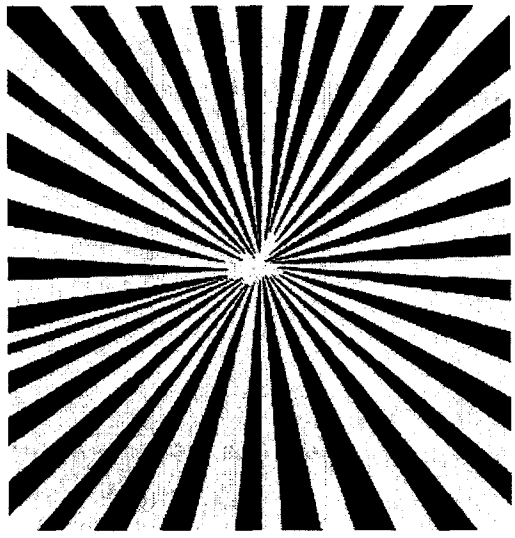
Images are seen both by blind subjects and in sealed dark rooms.

Images are stable with respect to eye movements

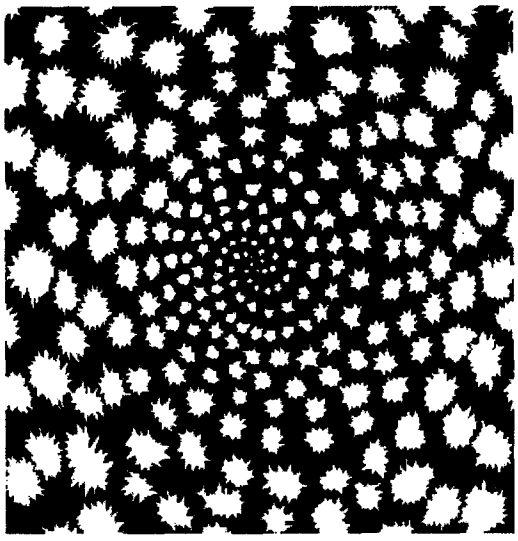
Recent studies suggest that areas V1 and V2 are involved in *visual imagery*.

Hypothesis II: The action of hallucinogens on those brain stem nuclei that control cortical excitability induce the spontaneous formation of cortical patterns of activity in V1.

Hypothesis III: Since all observers report seeing Klüver's form constants or variations, those properties common to all such hallucinations should yield information about the architecture of V1. In particular, they should reflect any symmetries of V1.



(I)



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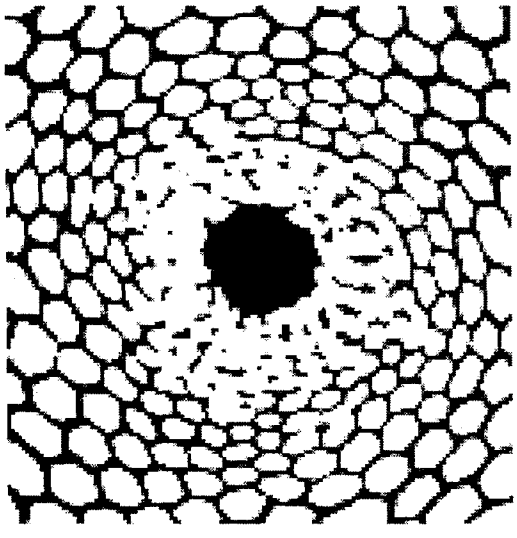

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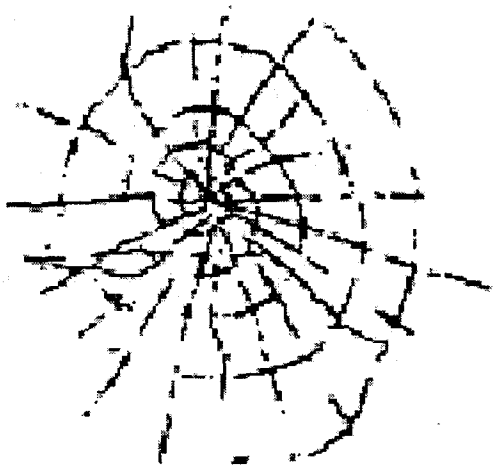


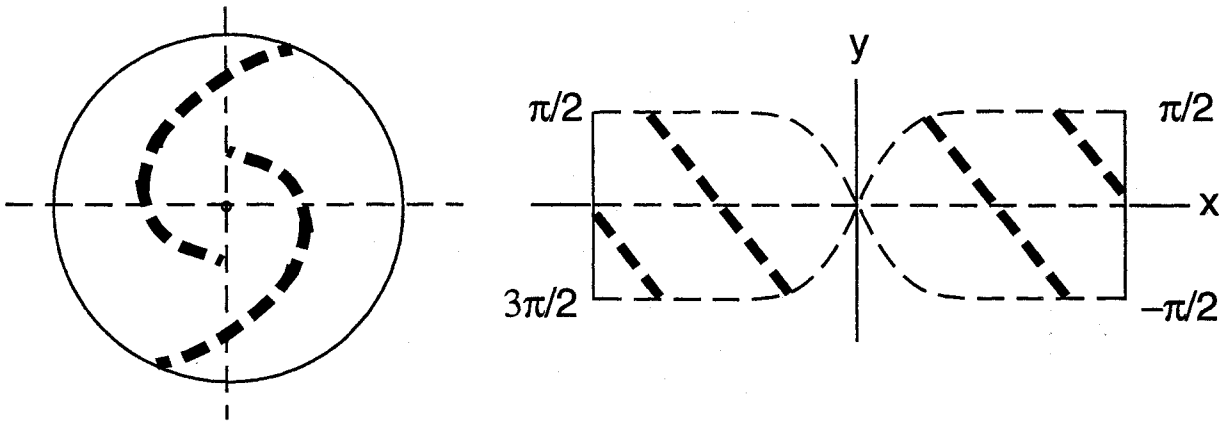
(IV)

Figure 1: (I) funnel and (II) spiral images induced by LSD, (III) honeycomb generated by marihuana, (IV) cobweb petroglyph

The retino-cortical map

• Away from the fovea, $1^o \leq r_R \leq 30^o$, the retino-cortical map is a *complex logarithm*

$$x = \frac{1}{\epsilon} \ln \frac{\epsilon r_R}{w_0}, \qquad y = \frac{\theta_R}{\epsilon}.$$



• If ϕ_R is the orientation of a line in the visual field, then:

$$\phi = \phi_R - \theta_R$$

i.e. local orientation in the visual cortex is *relative* to the angular coordinate of visual field position.

Form constants as spontaneous cortical patterns

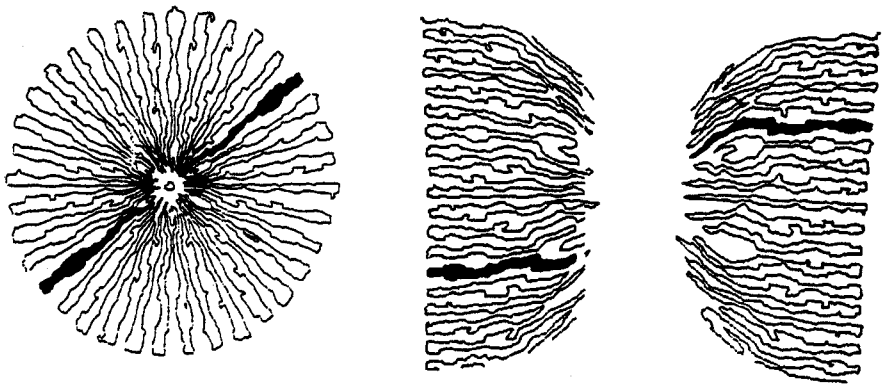


Figure 2: Action of the retino–cortical map on the funnel form constant.

- Form constants comprising circles, rays, and logarithmic spirals, in the visual field correspond roughly to *stripes* of neual activity at various angles in V1.

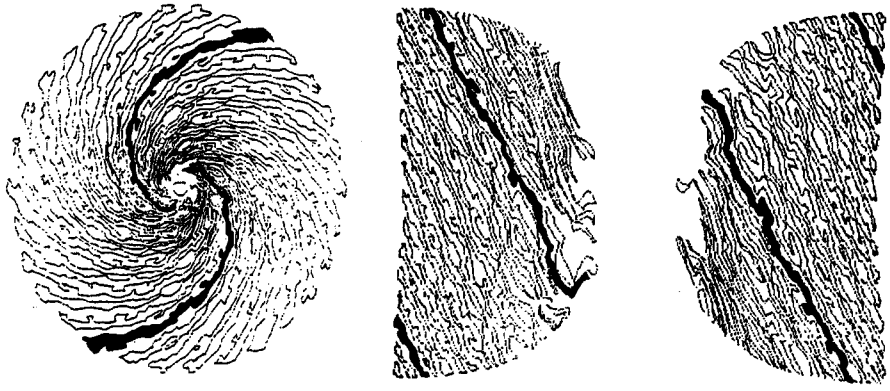
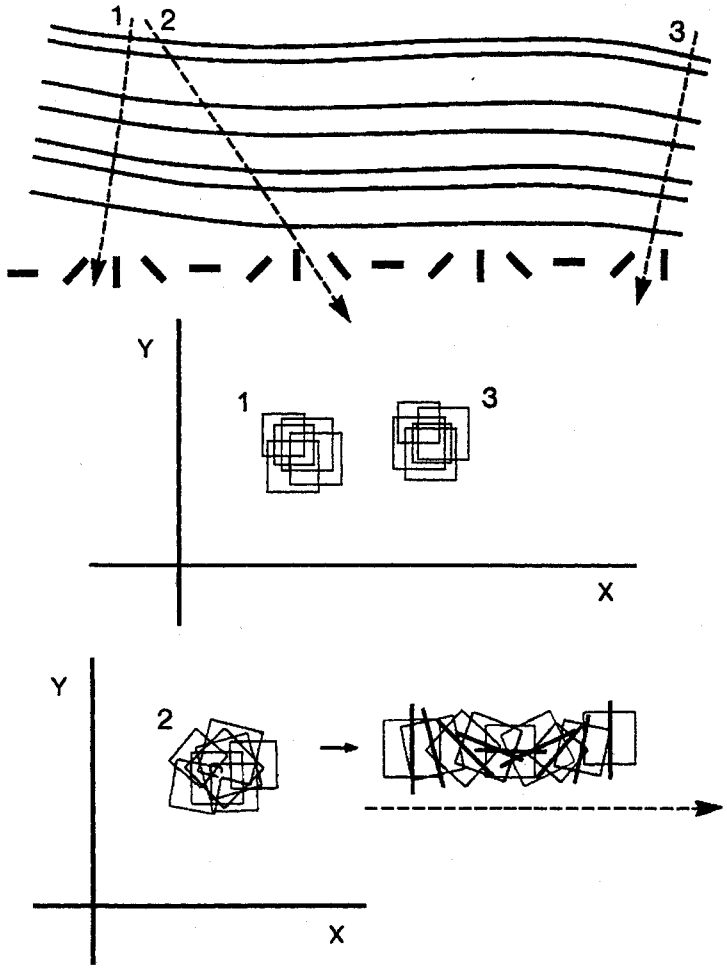


Figure 3: Action of the retino–cortical map on the spiral form constant.

Orientation tuning in V1

- Most V1 cells not only signal position in the visual field but also the local *orientation* of a contrast edge or bar (Hubel and Wiesel 1962)



• The distribution of orientation preferences is roughly π–periodic – approximately every millimeter there is an *iso–orientation patch* of a given preference

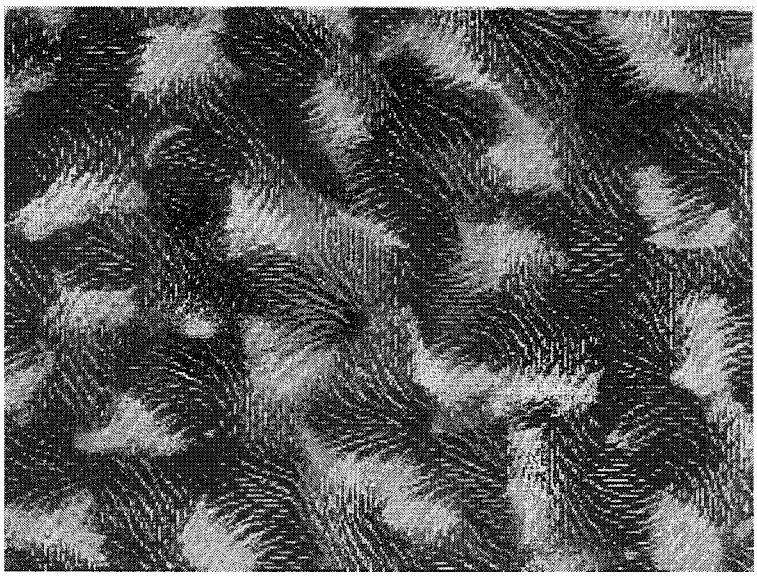


Figure 4: Distribution of orientation preferences in V1 obtained via optical imaging. Redrawn from Blasdel (1992).

• A *hypercolumn* is a region of V1 roughly $1.5mm \times 1mm$ on its surface and extending throughout its depth with two sets of iso-orientation patches in the range $0 \leq \phi < \pi$, one for each eye. Approximately $36 \times 36 = 1296$ such hypercolumns per hemifield.

- At least two interaction length–scales:

(a) *local connections* – cells less than a millimeter apart tend to make connections with most of their neighbors in a roughly isotropic fashion

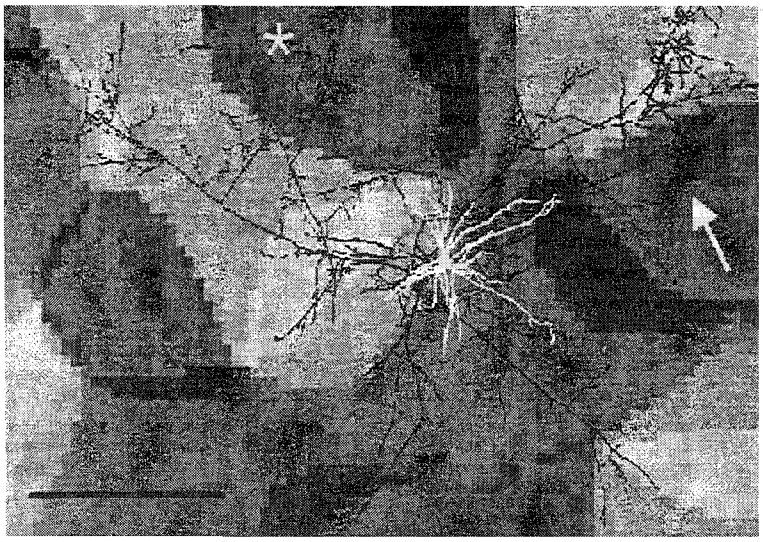


Figure 5: Connections made by an inhibitory interneuron in V1 (Das and Gilbert).

(b) *intrinsic lateral connections* – cells make patchy connections every millimeter or so along their axons with cells in similar iso–orientation patches. Such connections are found mainly in layers II and III of V1 and tend to run parallel to the visuotopic axis of their cell's orientation preference.

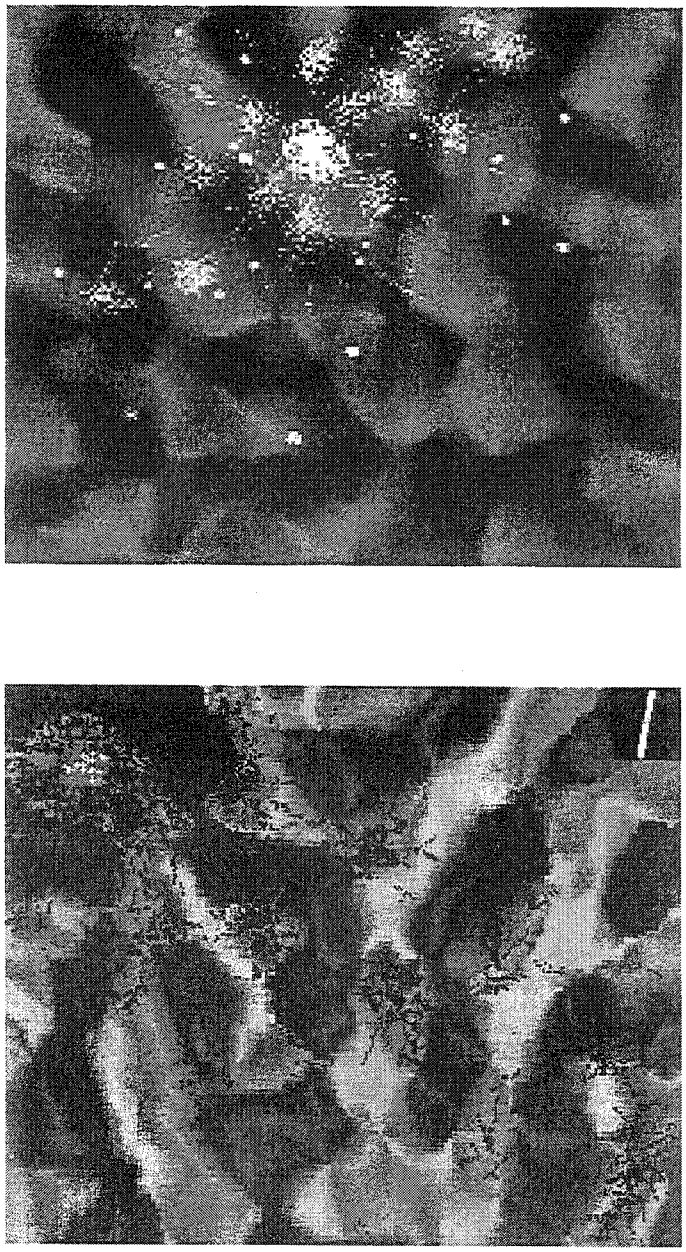
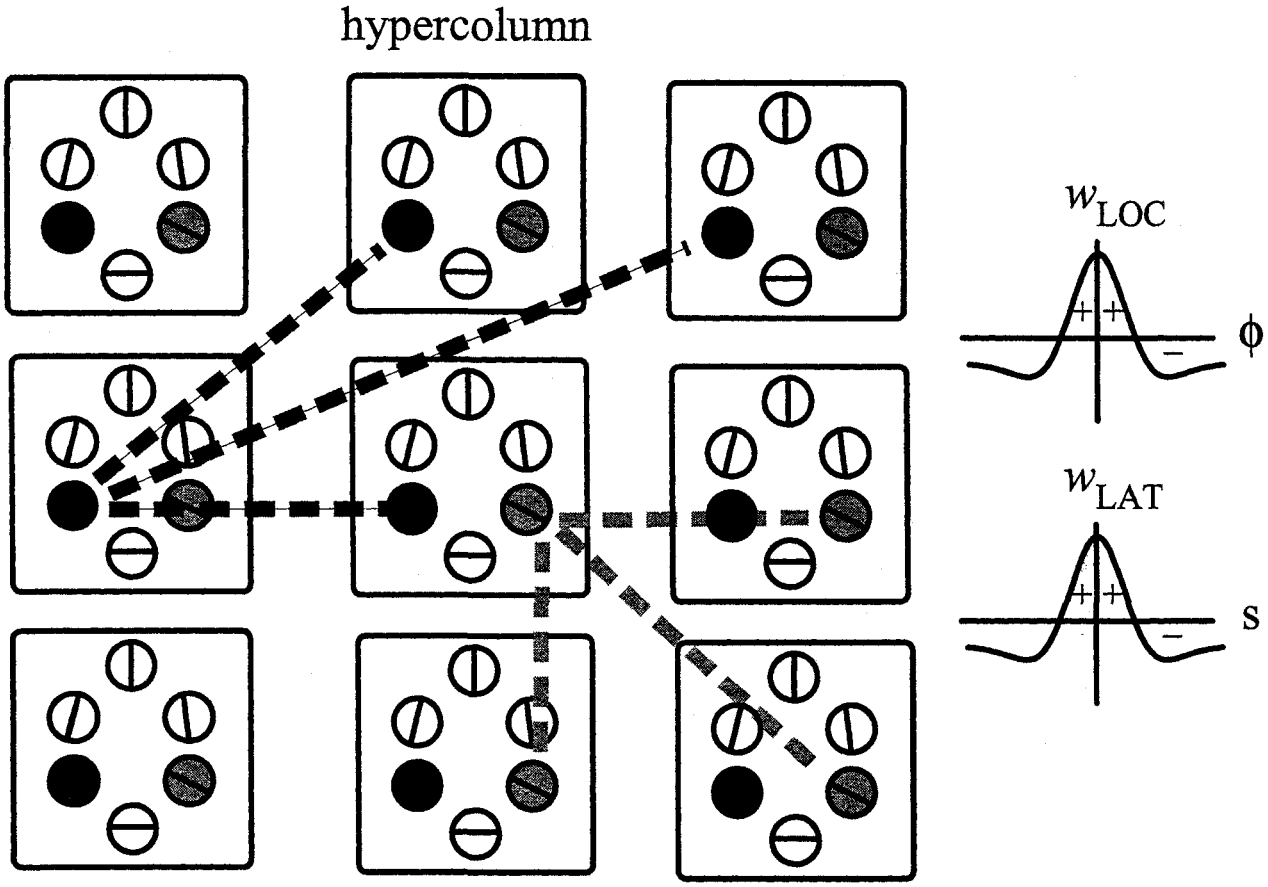


Figure 6: Lateral Connections made by a cell in V1. A radioactive tracer is used to show the locations of all terminating axons from cells in a central injection site, superimposed on an orientation map obtained by optical imaging (Blasdel [Personal Communication] and Bosking *et al* (1997))

A new cortical model



$$\frac{\partial a(\mathbf{r},\phi)}{\partial t} = -\alpha a(\mathbf{r},\phi) + \mu \int_0^{\pi} w_{LOC}(\phi-\phi')\sigma[a(\mathbf{r},\phi')]\frac{d\phi'}{\pi} + \nu \int_{\phi-\theta_0}^{\phi+\theta_0}\int_{-\infty}^{\infty} w_{LAT}(s)\sigma[a(\mathbf{r}+s\mathbf{e}_\theta,\phi)]d\theta ds$$

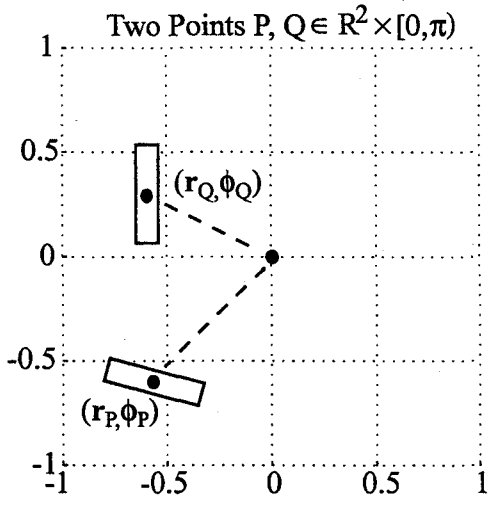
Euclidean symmetry

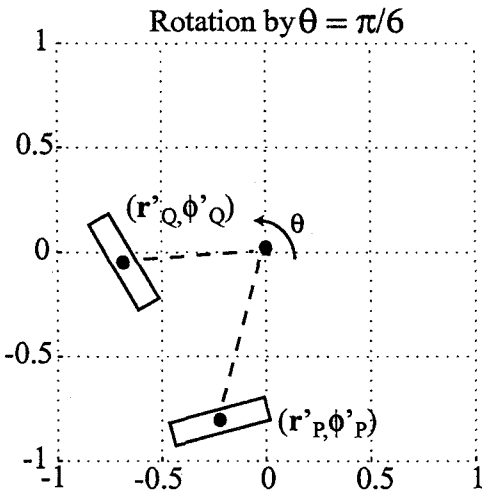
• Define the novel (*shift-twist*) action of the Euclidean group on $\mathbf{R}^2 \times \mathbf{S}^1$ by

$$\begin{aligned} \mathbf{s} \cdot (\mathbf{r}, \phi) &= (\mathbf{r} + \mathbf{s}, \phi) \quad \mathbf{s} \in \mathbf{R}^2 \\ \theta \cdot (\mathbf{r}, \phi) &= (R_\theta \mathbf{r}, \phi + \theta) \quad \theta \in \mathbf{S}^1 \\ \kappa \cdot (\mathbf{r}, \phi) &= (\kappa \mathbf{r}, -\phi), \end{aligned}$$

where κ is the reflection $(x_1, x_2) \mapsto (x_1, -x_2)$ and R_θ is the rotation matrix

$$R_\theta \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \cos\theta & -\sin\theta \\ \sin\theta & \cos\theta \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}.$$





Turing instability

• Let $a(\mathbf{r}, \phi) = 0$ be a stationary solution of the evolution equation. This homogeneous state is stable for all μ less than a critical value μ_c.

• The homogeneous state will destabilize if μ crosses μ_c. This could occur when the excitability of V1 increases due to the action of hallucinogens on brain stem nuclei such as the locus coerelus or the raphe nucleus, which secrete the monamines serotonin and noradrenalin.

• If μ remains close to μ_c then new stationary states develop that are approximated by (finite) linear combinations of eigenfunctions of the linearized evolution equation.

• The *equivariant branching lemma* guarantees the existence of new states with the symmetry of certain subgroups of the Euclidean group.

Eigenfunctions of V1

- Solutions of the form $a(\mathbf{r}, \phi, t) = a(\mathbf{r}, \phi)\mathrm{e}^{\lambda t}$
- Expand in powers of $\beta = \nu/\mu \ll 1$ and use degenerate perturbation theory to solve eigenvalue equation.
- To lowest order in β the eigenvalues are

$$\lambda_{\pm}(p, q) = -\alpha \left[1 - \frac{\mu}{\mu_{\pm}(p, q)}\right]$$

with

$$\mu_{\pm}(p, q) = W_{LOC}(p) + \beta \left\{W_{LAT}(0, q) \pm W_{LAT}(2p, q)\right\}$$

Here $W_{LOC}(p)$ is the pth Fourier mode of $w_{LOC}(\phi)$ and

$$W_{LAT}(p, q) = (-1)^p \frac{\sin(2p\theta_0)}{2p\theta_0} \int_0^{\infty} w_{LAT}(s) J_{2p}(qs) ds$$

where J_{2p} is a Bessel function and θ_0 determines the spread of lateral connections

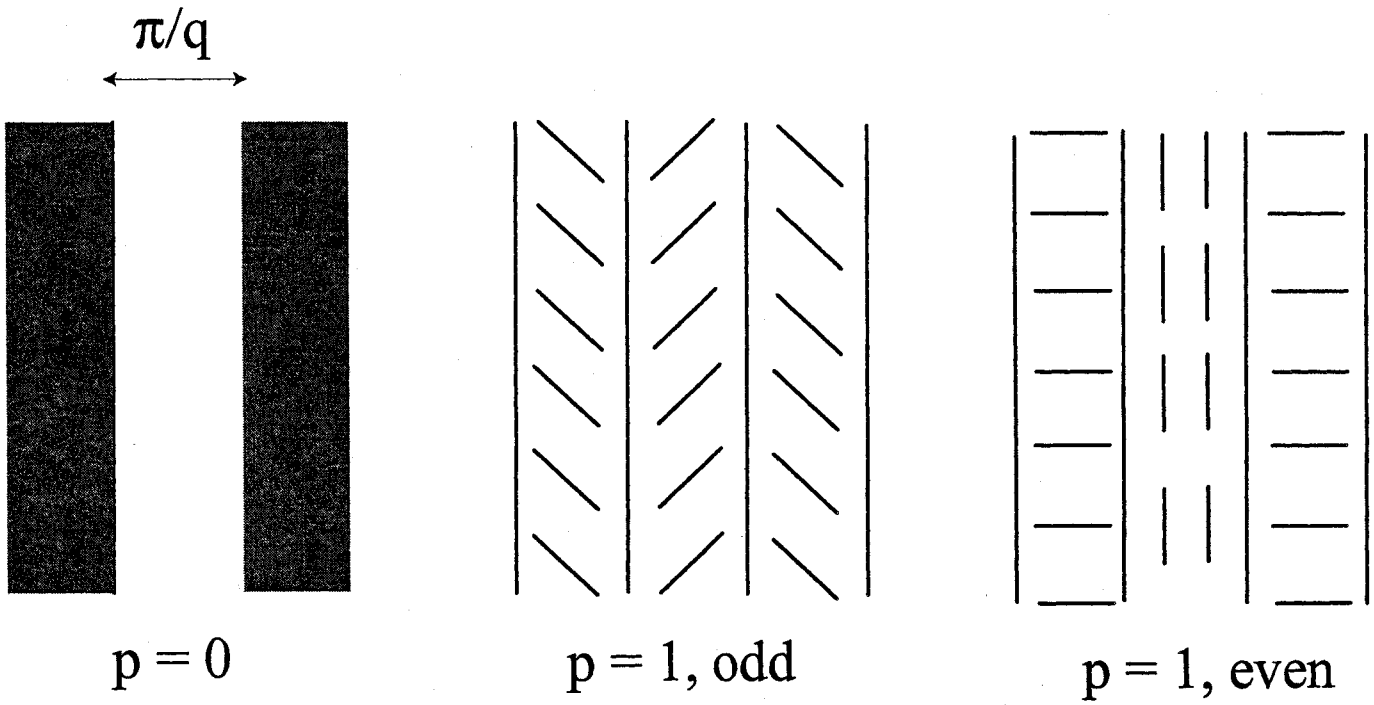
- Associated eigenfunctions are

$$a(\mathbf{r}, \phi) = u_p^{\pm}(\phi - \varphi_n) \left[c_n e^{i\mathbf{k}_n \cdot \mathbf{r}} + c_n^* e^{-i\mathbf{k}_n \cdot \mathbf{r}} \right]$$

with $\mathbf{k}_n = q(\cos\varphi_n, \sin\varphi_n)$ and to lowest order in β

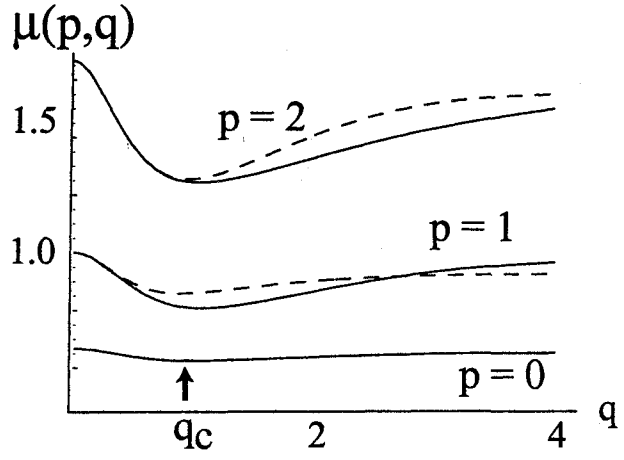
$$u_p^+(\phi) = \cos 2p\phi, \quad u_p^-(\phi) = \sin 2p\phi$$

- Represent plane waves modulated by even or odd phase-shifted π-periodic functions.

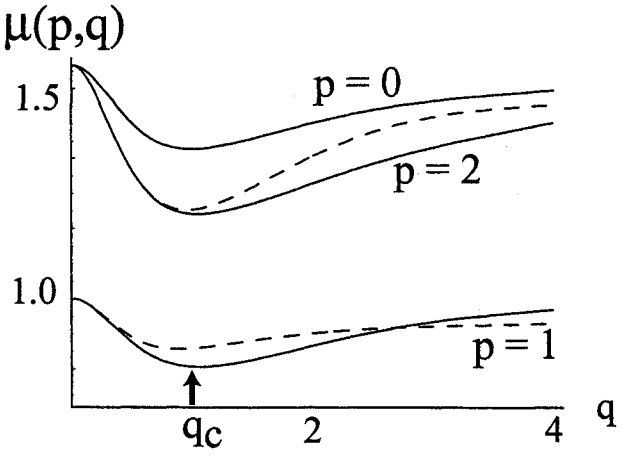


wavelength of stripe is $2\pi/q$ and direction is φ_n

Marginal stability curves



Hubel-Wiesel mode ($p_c = 0$)



Coupled-ring mode ($p_c > 0$)

- If $\mu < \mu_{\pm}(p, q)$ for all p, q then the homogeneous state is locally stable
- Critical coupling for a Turing instability is

$$\mu_c(p_c, q_c) = \min_{p,q,\pm}\{\mu_{\pm}(p, q)\}$$

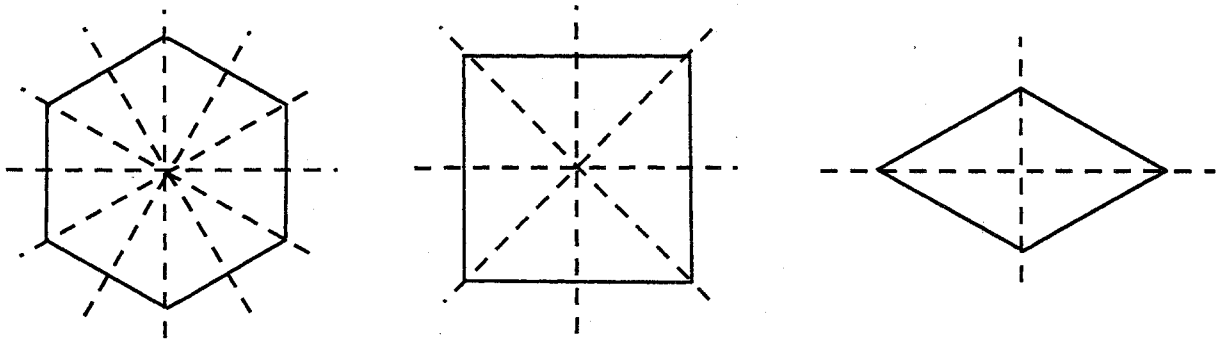
- ∞-degeneracy since all wavevectors $\mathbf{k}$ such that $|\mathbf{k}| = q_c$ are selected
- For small lateral spread ($\theta_0 < 45^o$) odd e-functions are selected otherwise even e-functions are selected.

Form constants as planforms

- Need to compute actual patterns of V1 that develop when the uniform state loses stability - linear combinations of critical eigenfunctions (planforms).
- Assume that planforms generate regular tilings of the plane by restricting to doubly periodic solutions: $a : \mathbf{R}^2 \times \mathbf{S}^1 \to \mathbf{R}$ is *doubly periodic* with respect to a planar lattice $\mathcal{L}$ if for every $\boldsymbol{\ell} \in \mathcal{L}$.

$$a(x + \boldsymbol{\ell}, \phi) = a(x, \phi)$$

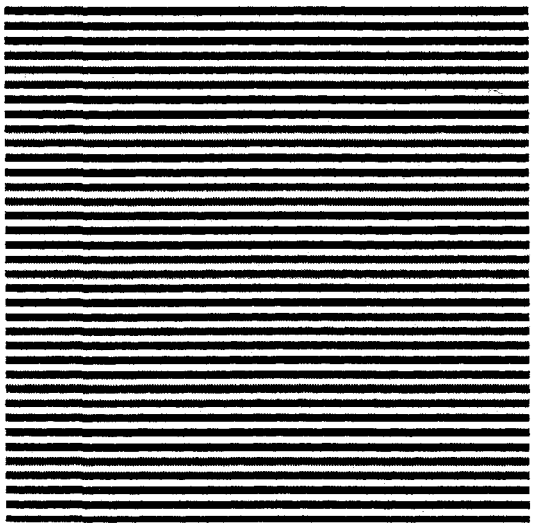
- Planforms then have either rhombic, square or



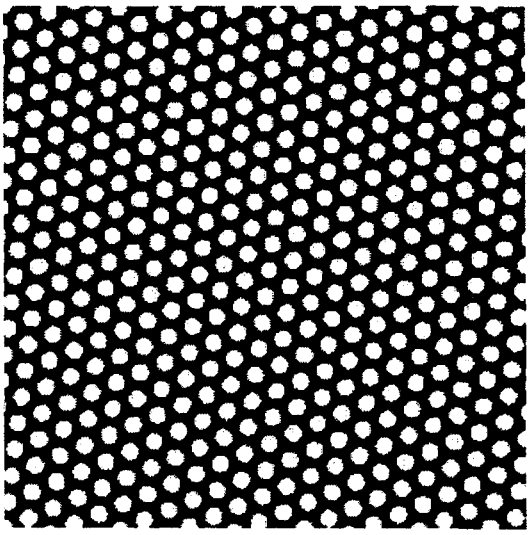
hexagonal symmetry. Finite combinations of plane waves ($\mathbf{k}$ lies on dual lattice of $\mathcal{L}$)

The equivariant branching lemma

- Each doubly periodic eigenfunction is invariant with respect to a *discrete* subgroup of E(2). If the eigenfunction is the only solution with such a symmetry, then it corresponds to an *axial subgroup* of E(2).
- The equivariant branching lemma shows that when the homogeneous state of a symmetric dynamical system becomes unstable, new solutions appear that (generically) have symmetries corresponding to the axial subgroups of the underlying system symmetry group.
- The axial subgroups are distinct for even and odd solutions



(I)



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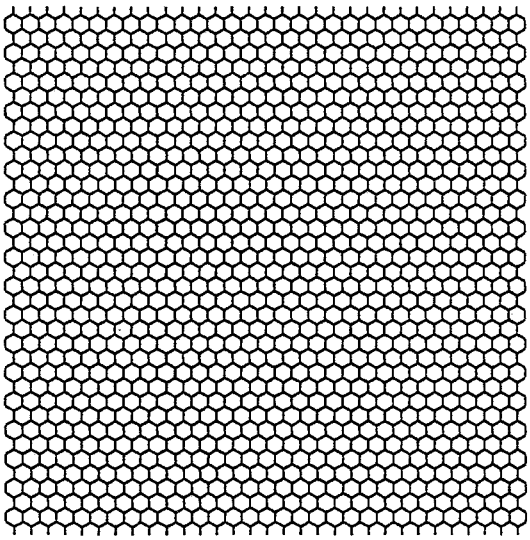

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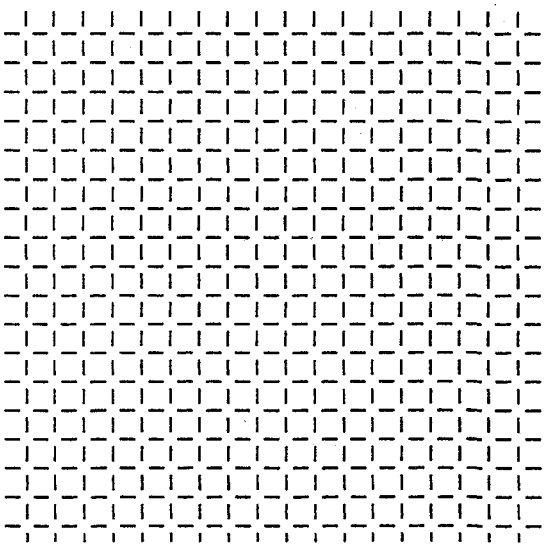
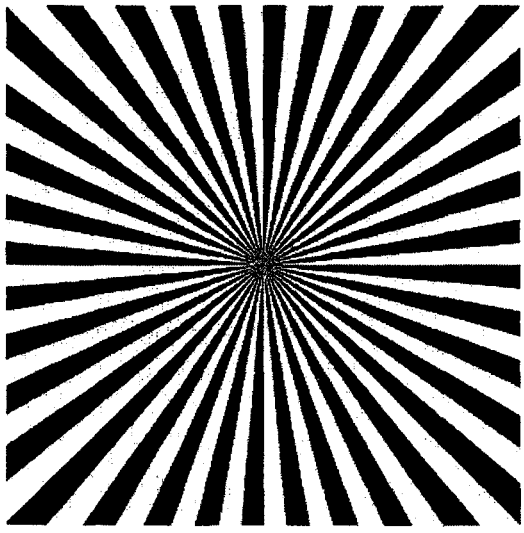
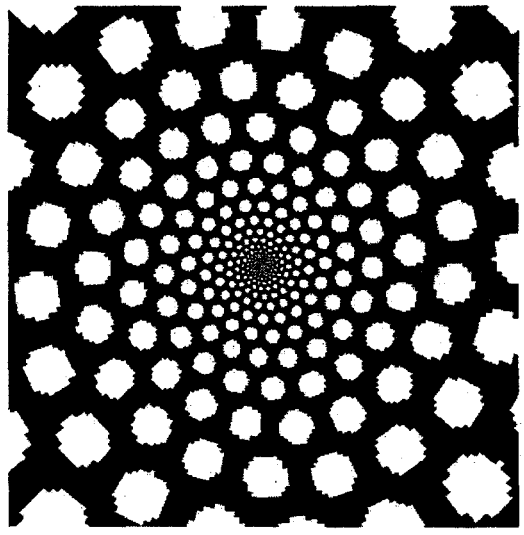


(IV)

V1 planforms



(I)



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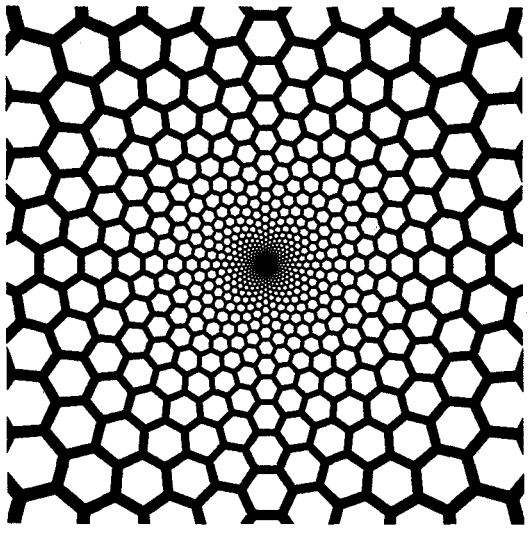
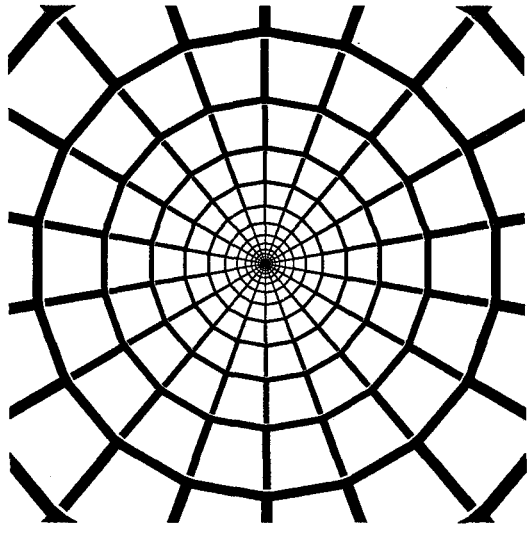


(III)



(IV)

Visual field planforms

Future directions

- Other feature maps:

  spatial frequency

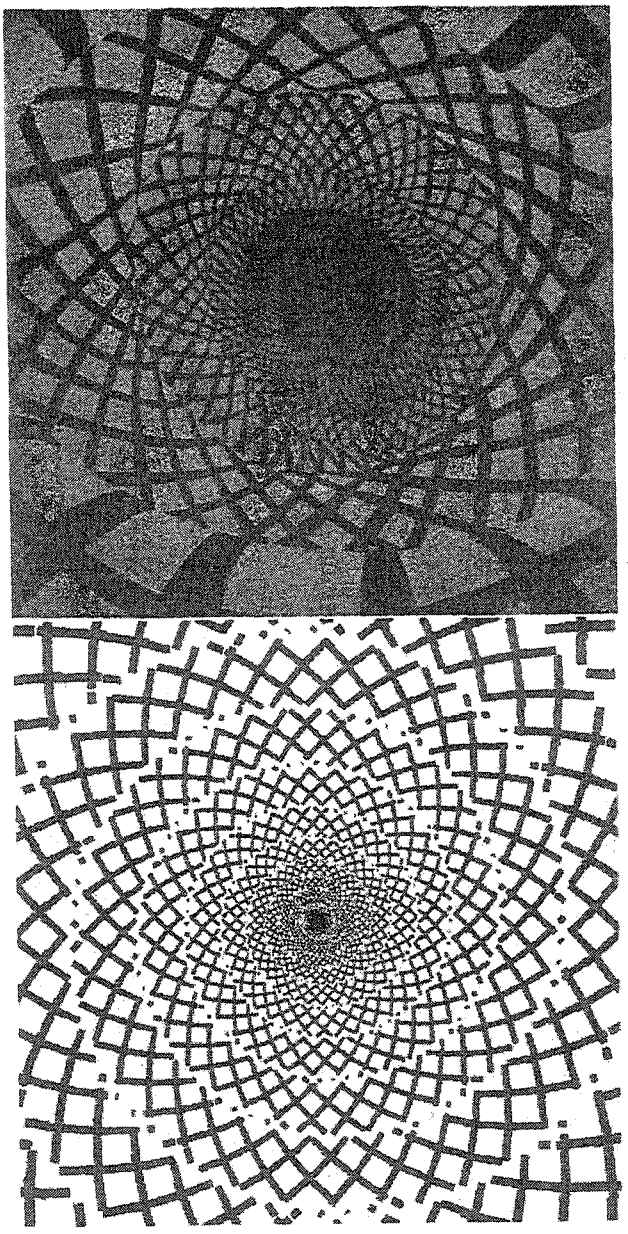
  ocular dominance

  binocular disparity

  color

  motion

- Contextual effects
- Layered structure of cortex: multi-population model
- Feedback from higher cortical areas
- Temporal dynamics



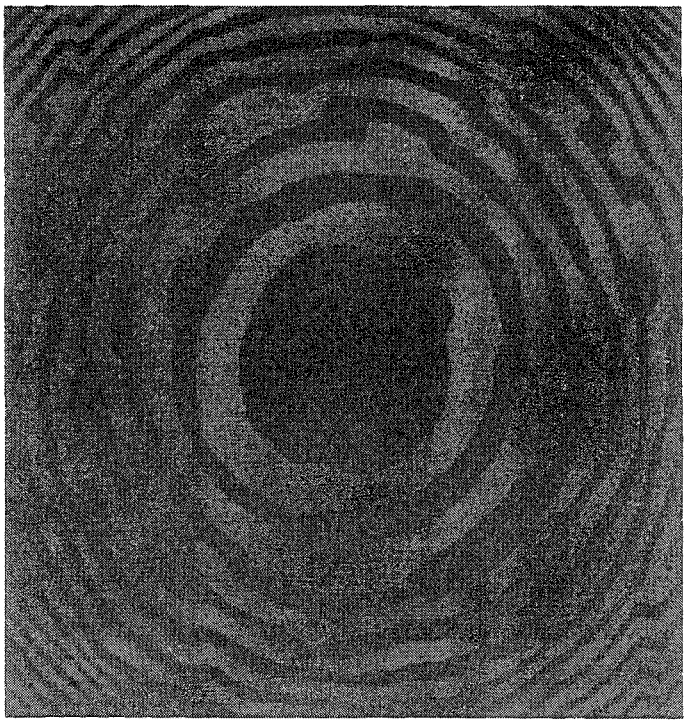


Figure 7: Tunnel hallucination generated by LSD (Oster 1970).

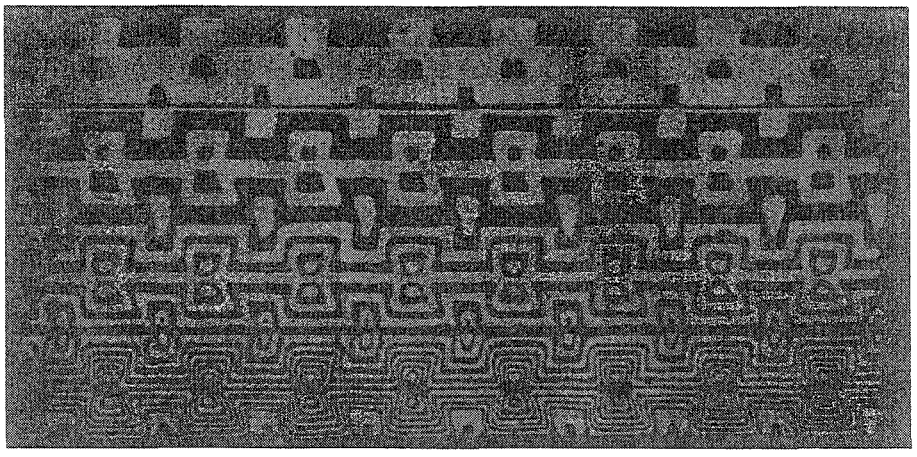
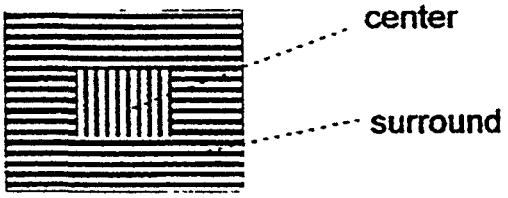
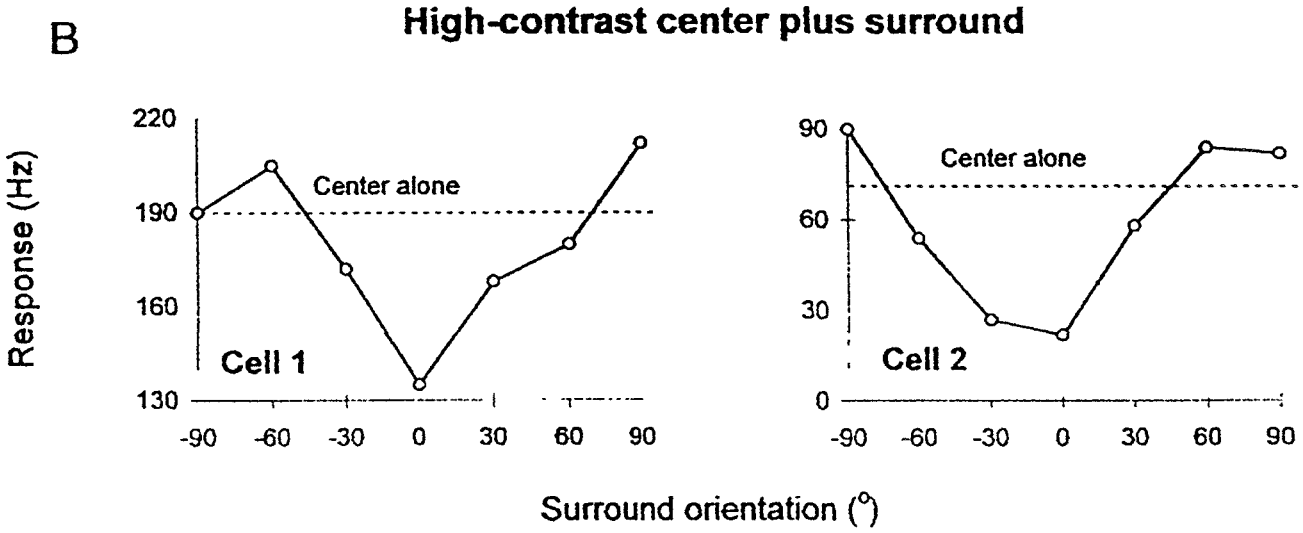


Figure 8: Complex hallucination generated by LSD (Oster 1970)

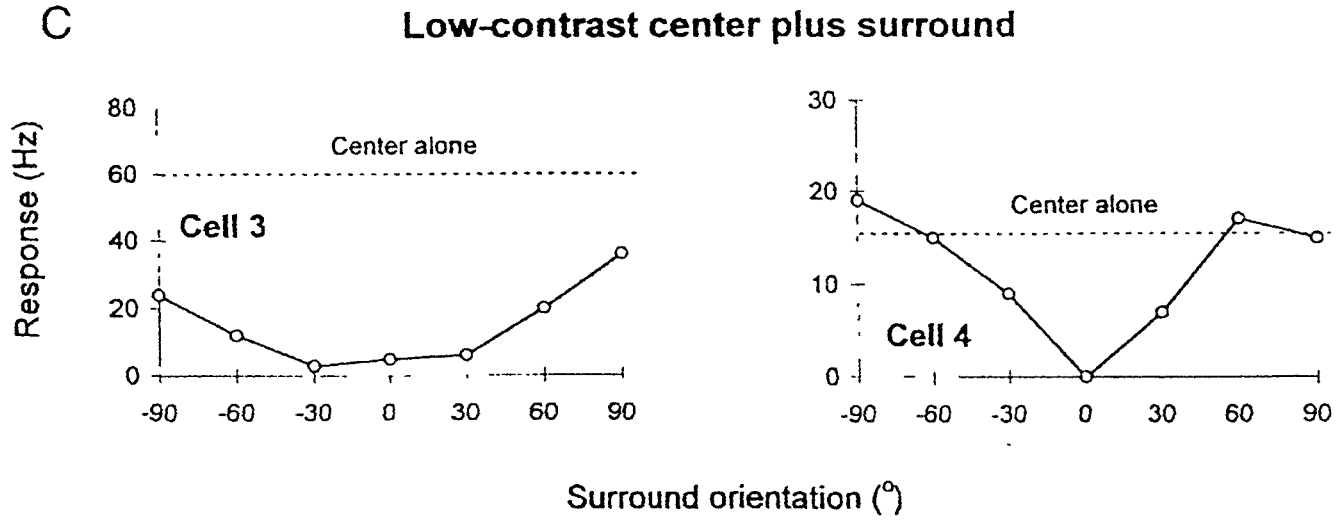
A


center
surround

B


High-contrast center plus surround
Response (Hz)
220
190
160
130
Center alone
Cell 1
90
60
30
0
Center alone
Cell 2
-90 -60 -30 0 30 60 90
-90 -60 -30 0 30 60 90
Surround orientation (°)

C

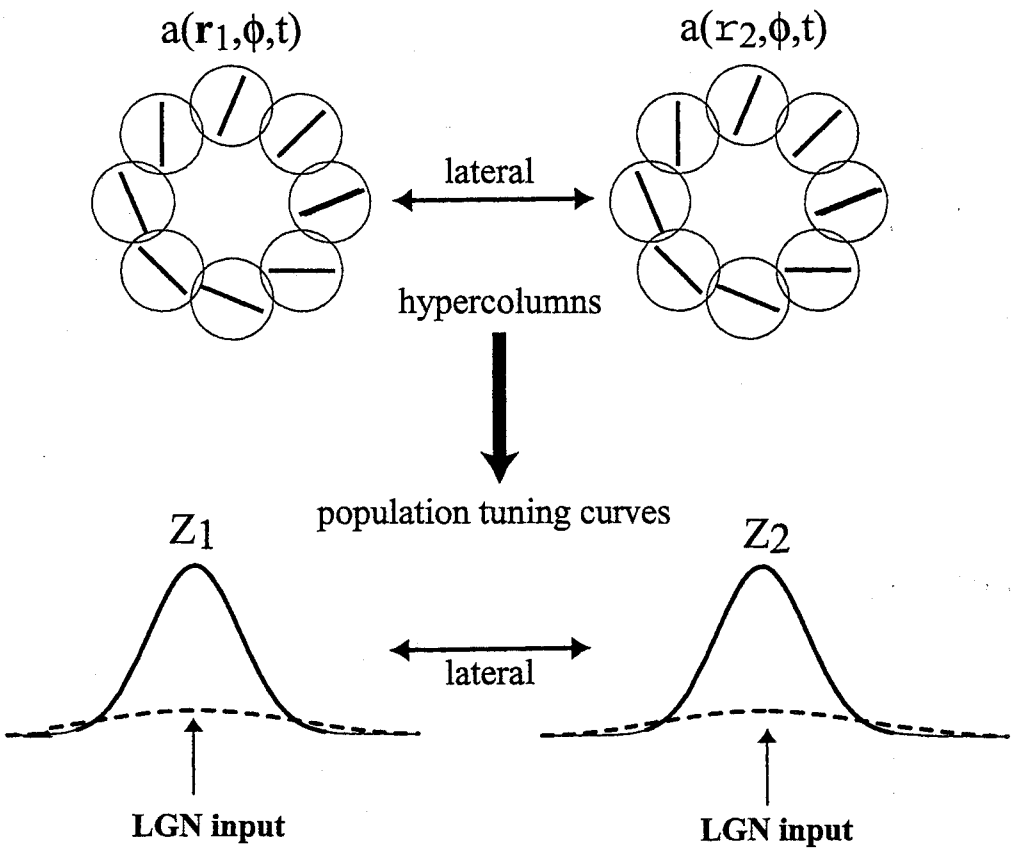

Low-contrast center plus surround
Response (Hz)
80
60
40
20
0
Center alone
Cell 3
30
20
10
0
Center alone
Cell 4
-90 -60 -30 0 30 60 90
-90 -60 -30 0 30 60 90
Surround orientation (°)

Coupled-ring mode revisited

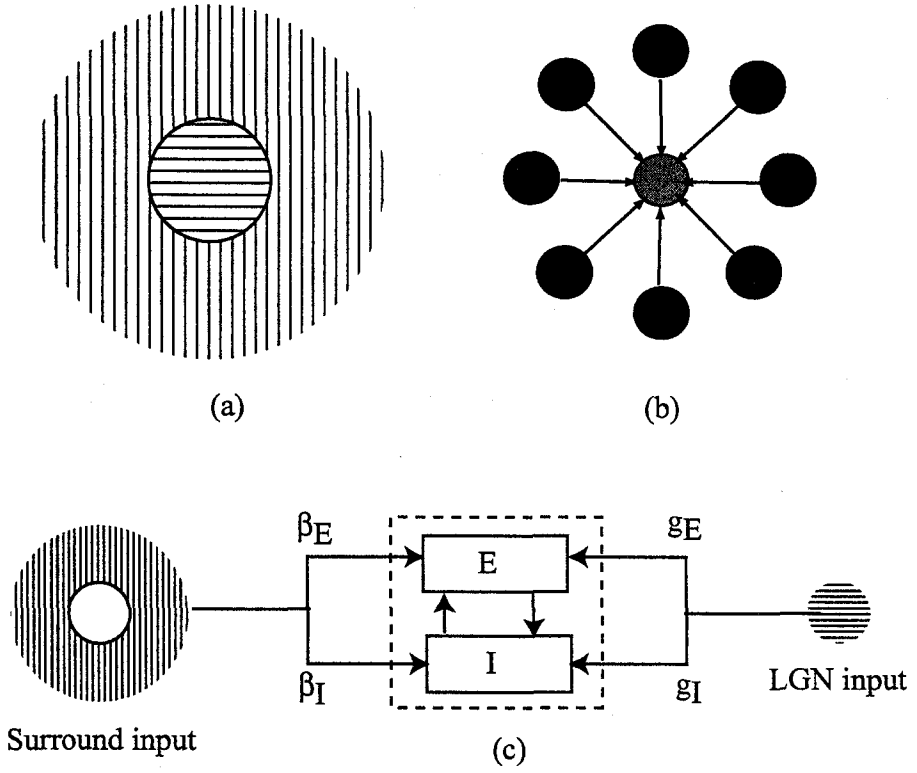
- Can reduce dynamics to a set of amplitude equations for the population tuning curves:

a) determine selection of planforms

b) determine modulatory effects of lateral interactions on response to LGN inputs - contextual effects



Center-surround modulation



(a) Circular center-surround stimulus configuration

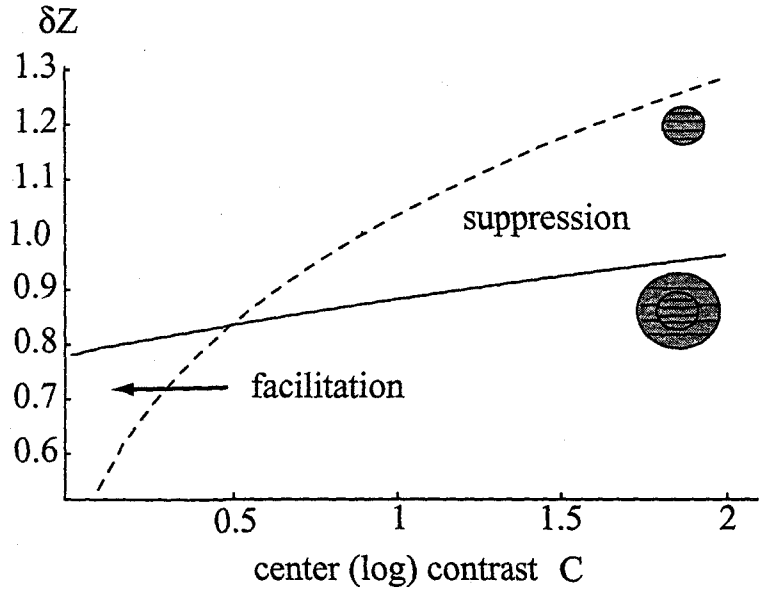
(b) Center hypercolumn interacting with a ring of surround hypercolumns

(c) Effective single-hypercolumn circuit

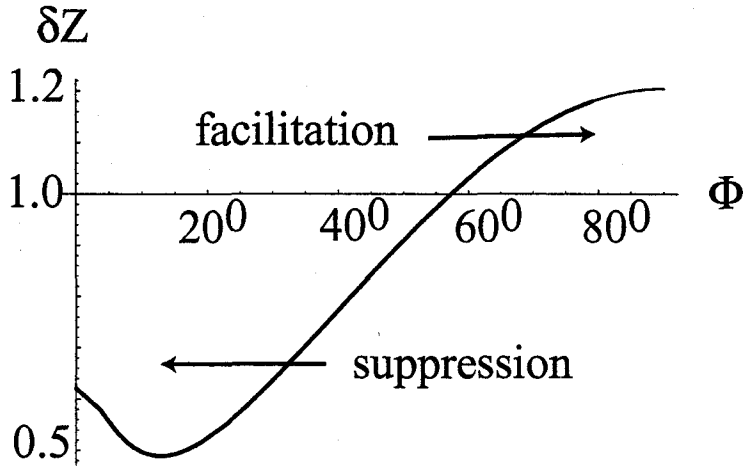
• If Z is amplitude of center hypercolumn then

$$\frac{\partial Z}{\partial \tau} = Z(\mu - |Z|^2) + LGN\ inputs + surround\ inputs$$

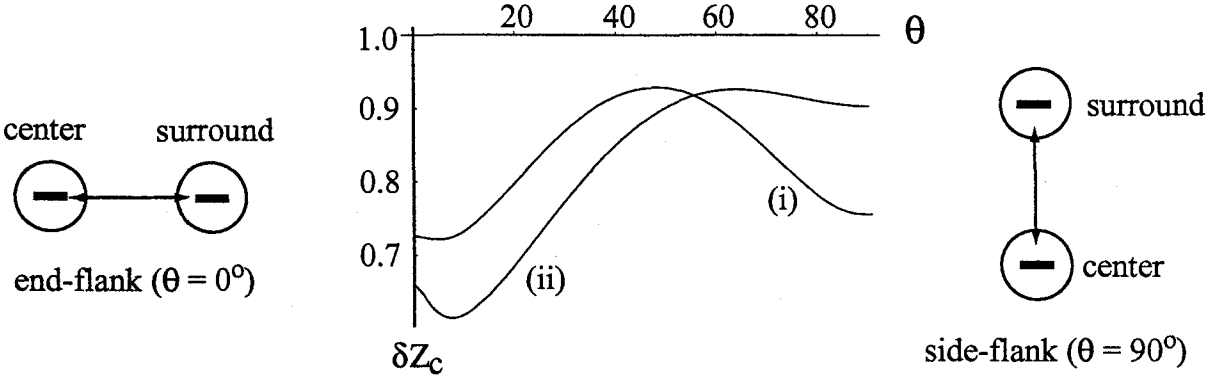
• Assume lateral interactions change from inhibitory to excitatory as contrast C of center stimulus is reduced. This induces a switch from suppression to facilitation for colinear center and surround.



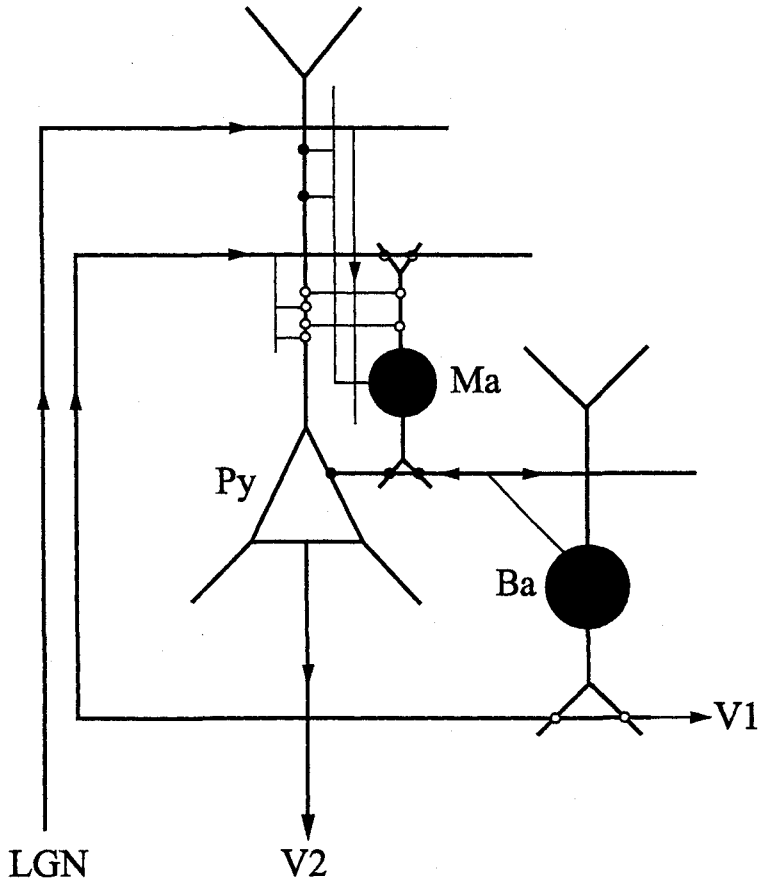
• Let Φ denote relative orientation of center and surround. Switch from suppression to facilitation as Φ is increased.

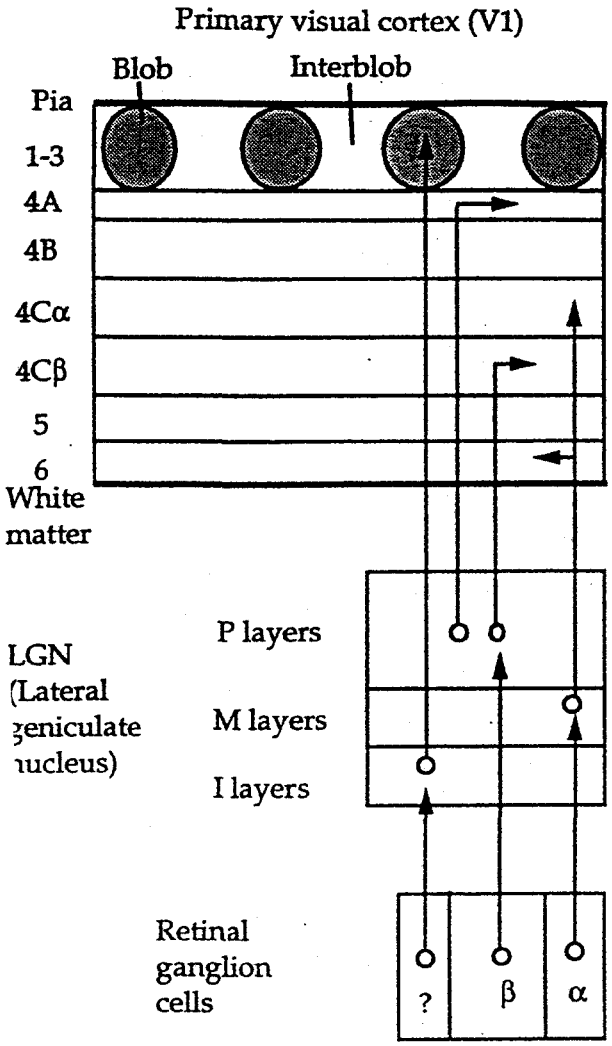


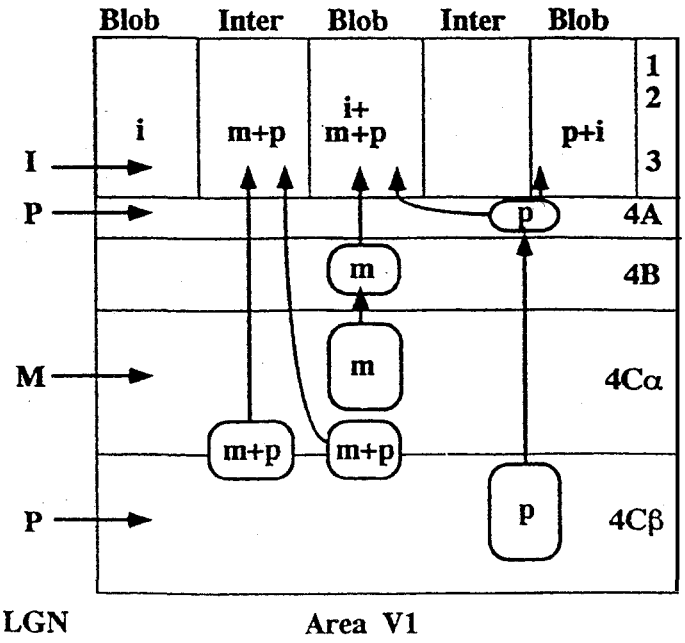
• Anisotropy of lateral interactions implies a dependence on the relative positions of center and surround stimuli.

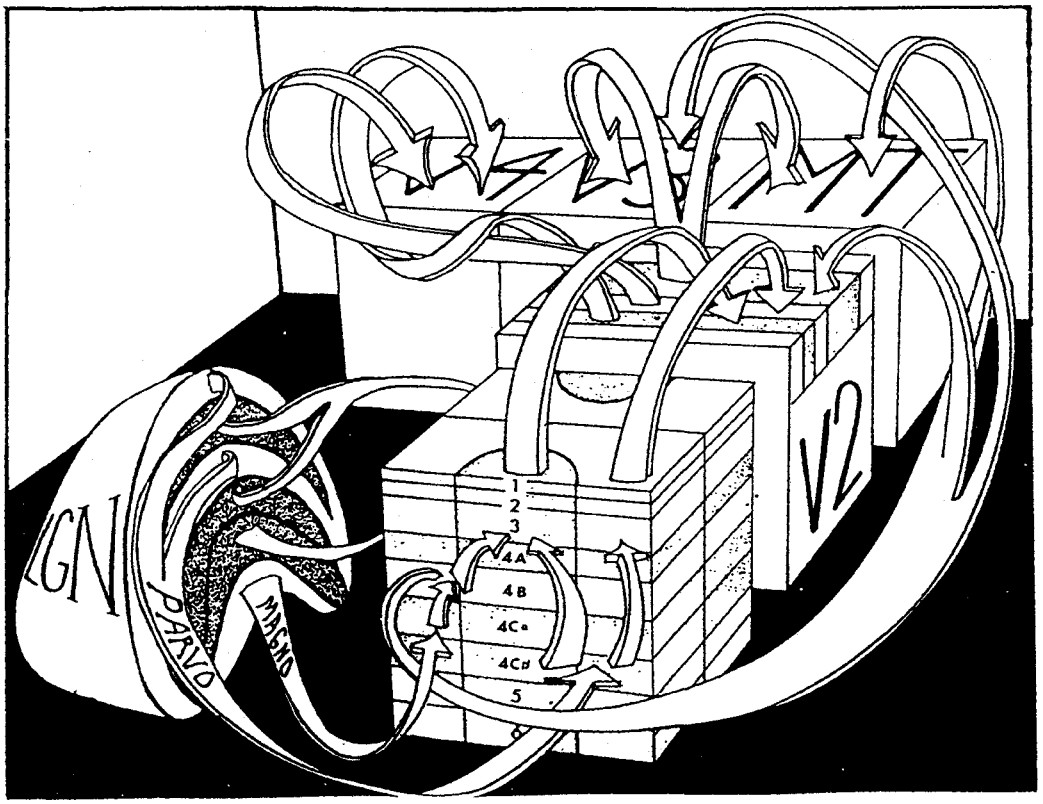


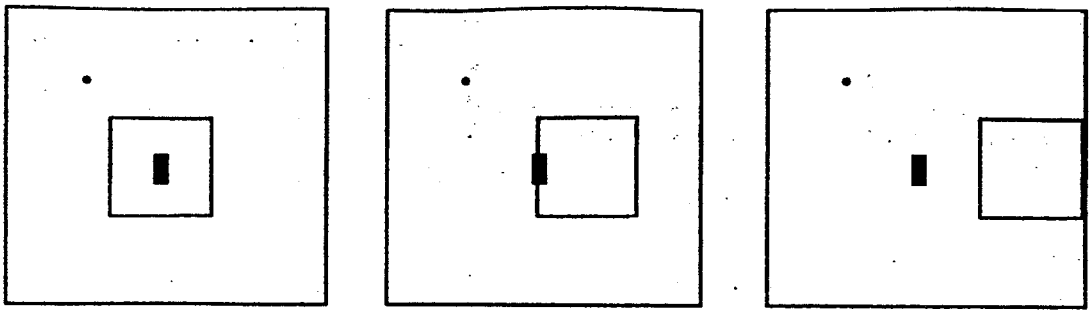
• Three population model distinguishes between interneurons with horizontally distributed axonal fields (basket cells) and those with predominantly vertically aligned axonal fields (martinotti, chandelier)



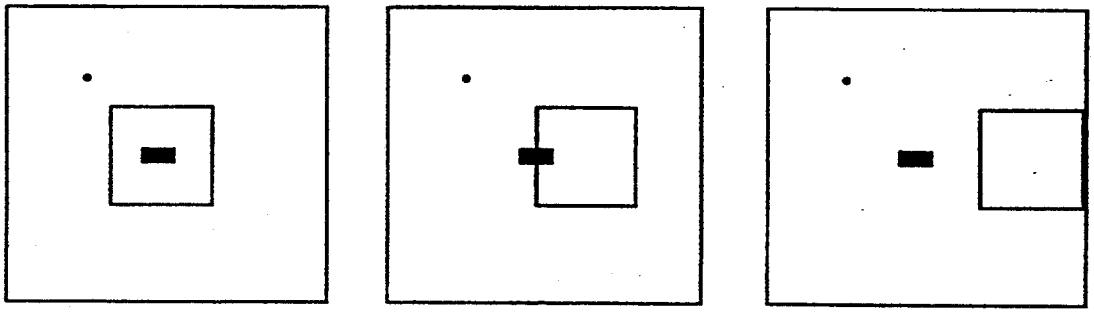

Primary visual cortex (V1)
Blob
Interblob
Pia
1-3
4A
4B
4Cα
4Cβ
5
6
White matter
LGN (Lateral geniculate nucleus)
P layers
M layers
I layers
Retinal ganglion cells
?
β
α


Blob
Inter
Blob
Inter
Blob
1
2
3
i
m+p
i+ m+p
p+i
I
P
M
P
4A
4B
4Cα
4Cβ
m
m
m+p
m+p
p
p
LGN
Area V1

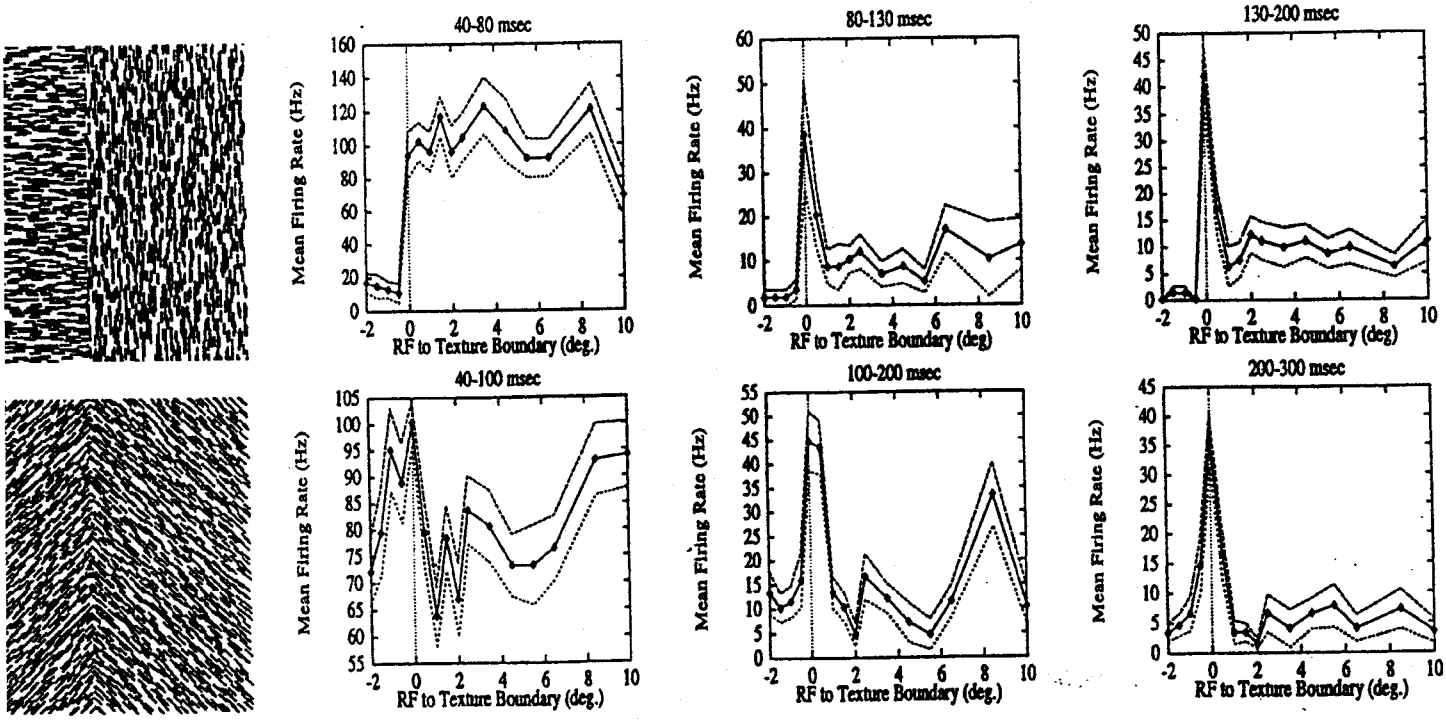

LGN
PARVO
MAGNO
V2
1
2
3
4A
4B
4Cα
4Cβ
5

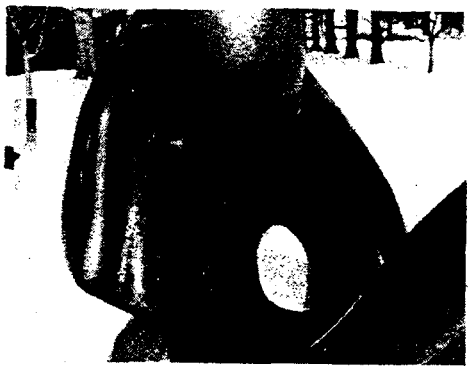


Center (Parallel Cond.) Boundary (Parallel Cond.) Outside (Parallel Cond.)



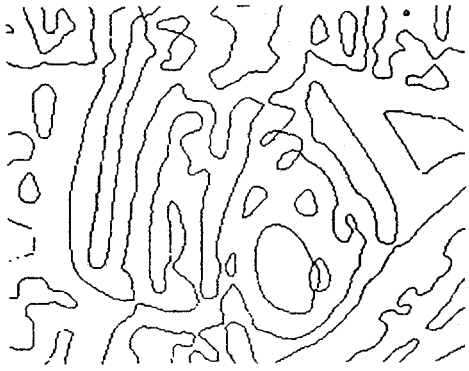
Center (Orthogonal Cond.) Boundary (Orthogonal Cond.) Outside (Orthogonal Cond.)



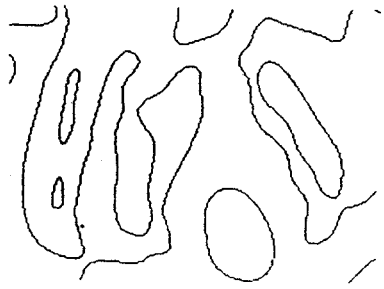


A

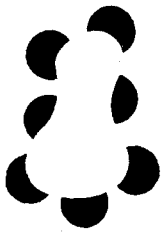
B



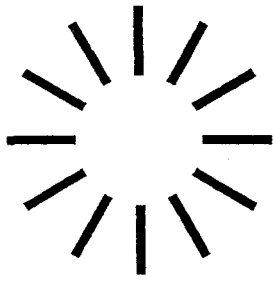
C



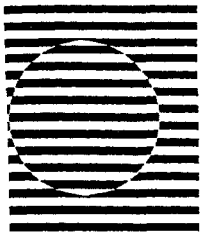
D



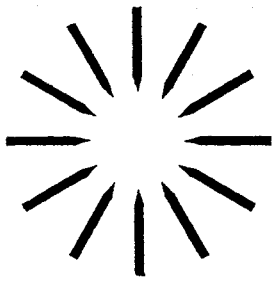
A



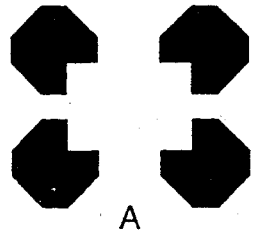
B



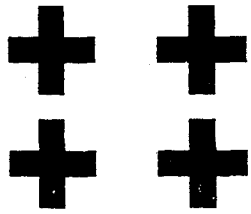
C



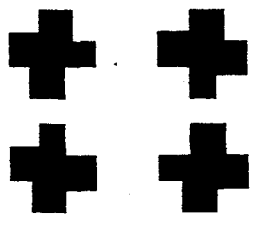
D



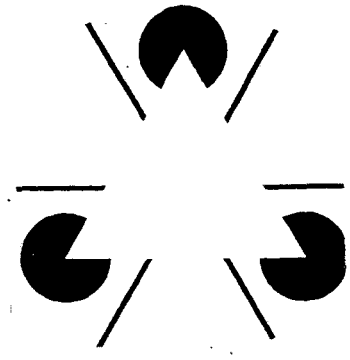
A

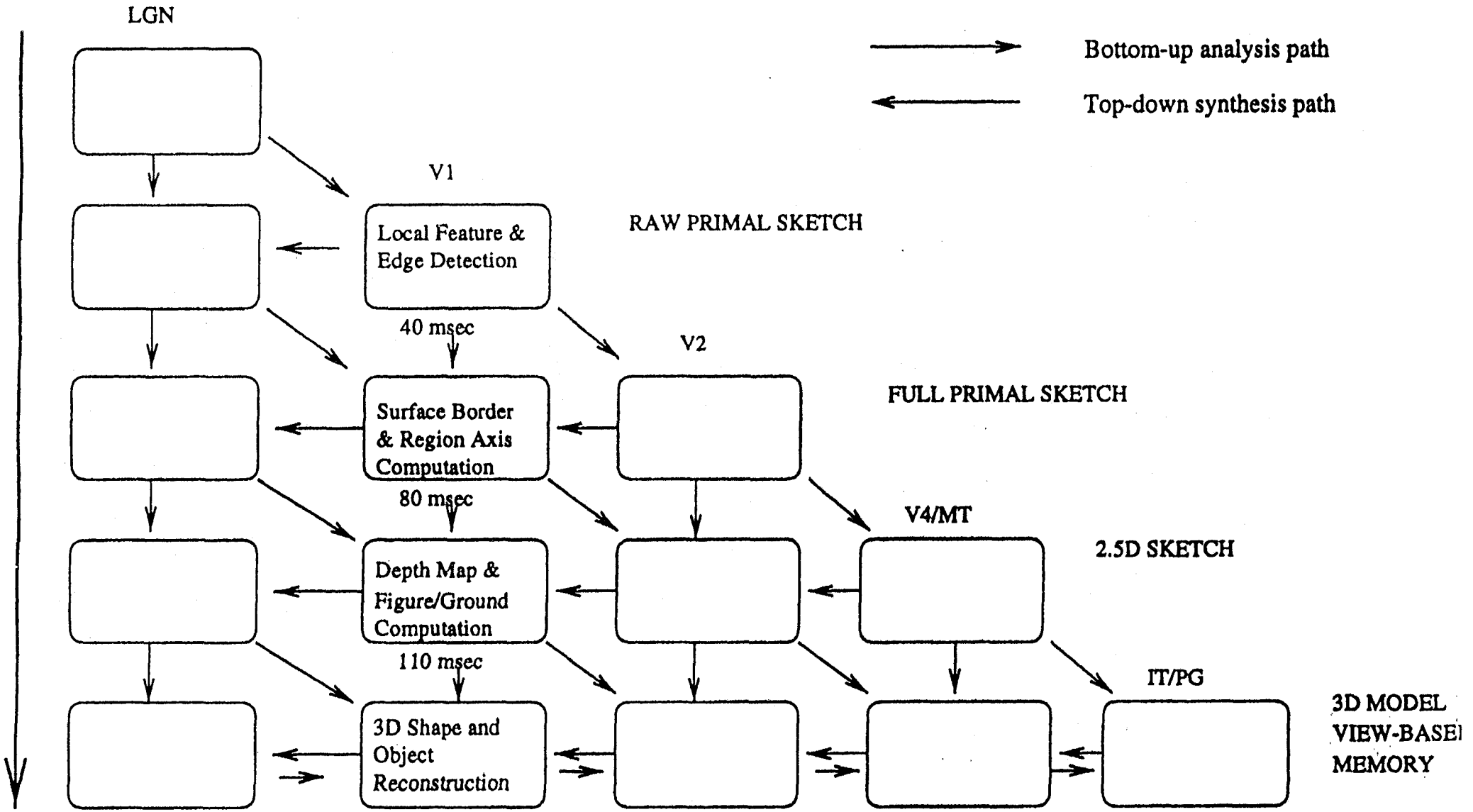


B



C




LGN
Bottom-up analysis path
Top-down synthesis path
V1
RAW PRIMAL SKETCH
Local Feature & Edge Detection
40 msec
V2
FULL PRIMAL SKETCH
Surface Border & Region Axis Computation
80 msec
V4/MT
2.5D SKETCH
Depth Map & Figure/Ground Computation
110 msec
IT/PG
3D MODEL VIEW-BASE MEMORY
3D Shape and Object Reconstruction