Séminaire Cerveau et Cognition
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Neurogéométrie de la vision

Architectures de calcul dans le cortex visuel

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Introduction

- What I call neurogeometry concerns the neural implementation of the geometric structures of visual perception.
- It concerns perceptive geometry "from within" and not 3D Euclidean geometry of the outside world.
- The general problem is to understand how the visual system can be a neural geometric engine.

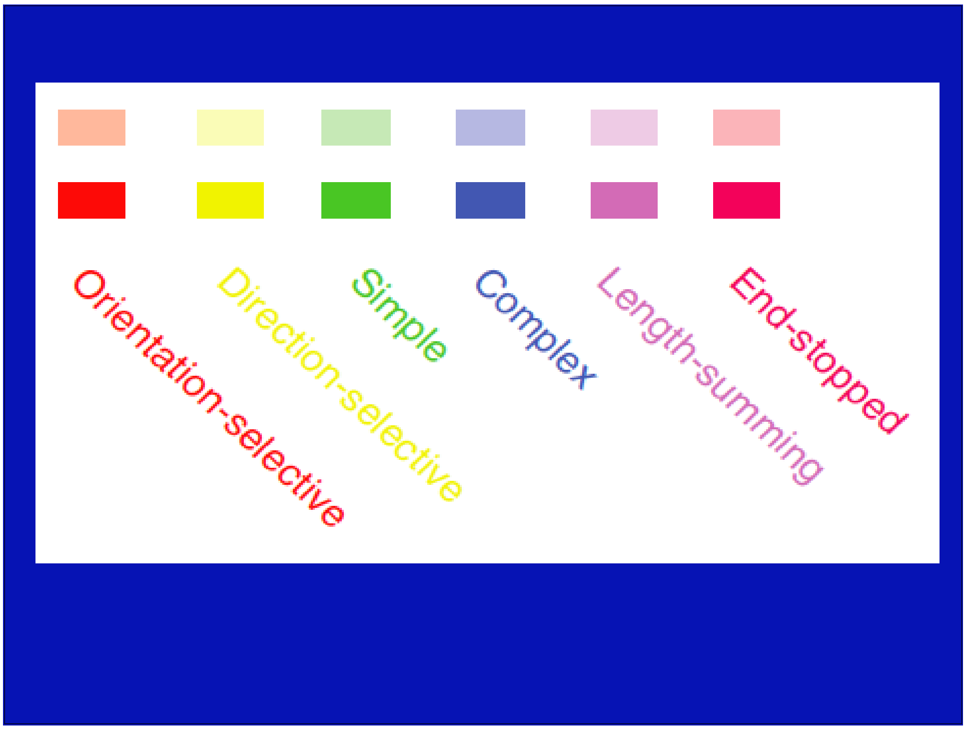
Limitations

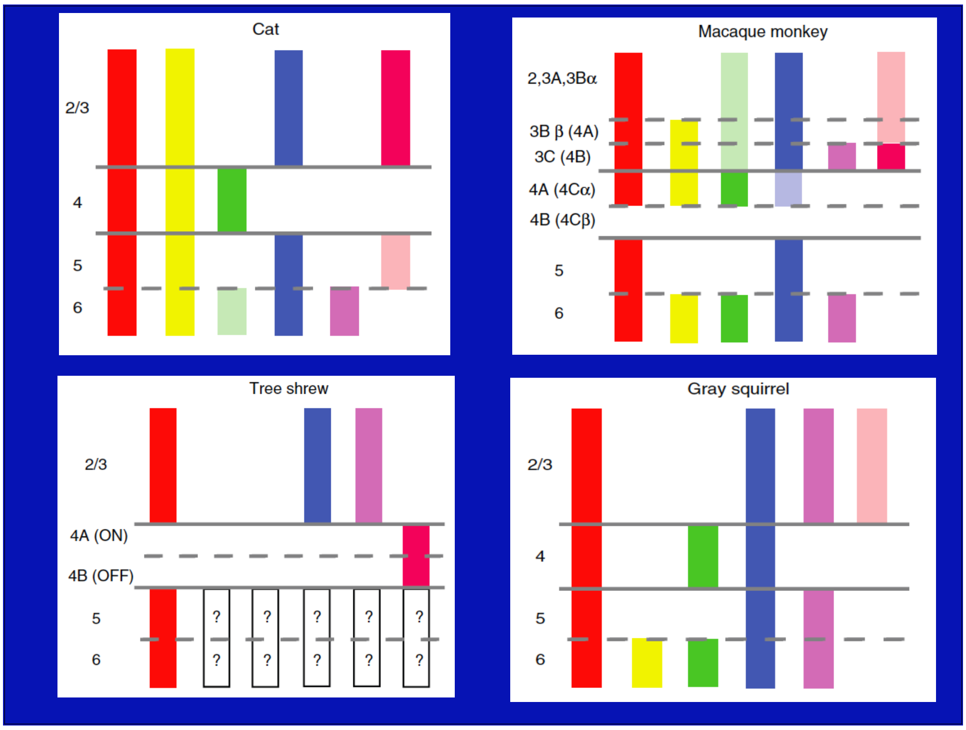
- We focus on V1, but there are of course many top-down feedbacks from other areas to V1.
- Neural implementation varies with species (rat, ferret, tree shrew, cat, macaque, man, etc.). The same functional architecture can be implemented in different ways.

- Stephen van Hooser on “Similarity and diversity" of V1 in mammals (comparative study).
- The gross laminar interconnections and the major functional responses are nearly invariant: 6 layers, LGN projecting mainly on the granular 4th layer.
- Three principal classes of LGN cells: parvocellular (P), magnocellular (M), koniocellular (K), etc.

- But the fine laminar structures are quite different.
- Tree shrew (Tupaya), Cat, Macaque have orientation maps with orientation hypercolumns and a functional “horizontal” architecture connecting neurons of similar orientation.
- Rat and Gray squirrel have not.

- Figure. Orientation simple cells (red) are absent in macaque 4B and tree shrew layer 4.
  - [[Direction selectivity dominates in the cat but is only common in specific layers of macaque and squirrel.
  - End-stopped VS lengthsumming cells : they decrease VS increase their responses as bars or gratings length increases.]]

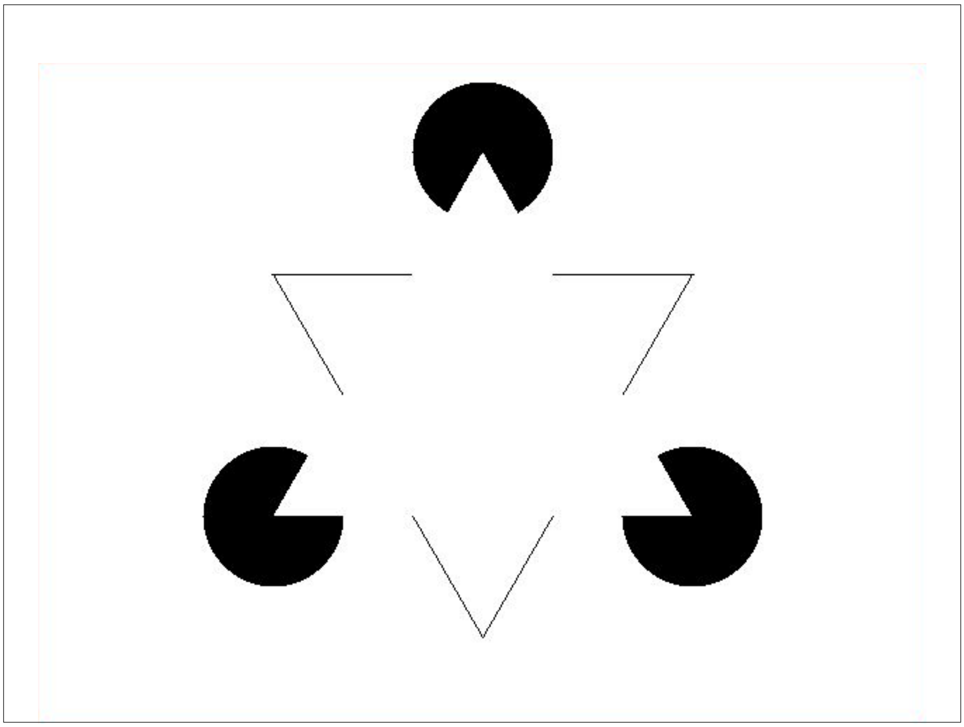

Orientation-selective
Direction-selective
Simple
Complex
Length-summing
End-stopped


Cat
2/3
4
5
6
Macaque monkey
2,3A,3Bα
3B β (4A)
3C (4B)
4A (4Cα)
4B (4Cβ)
5
6
Tree shrew
2/3
4A (ON)
4B (OFF)
5
6
Gray squirrel
2/3
4
5
6

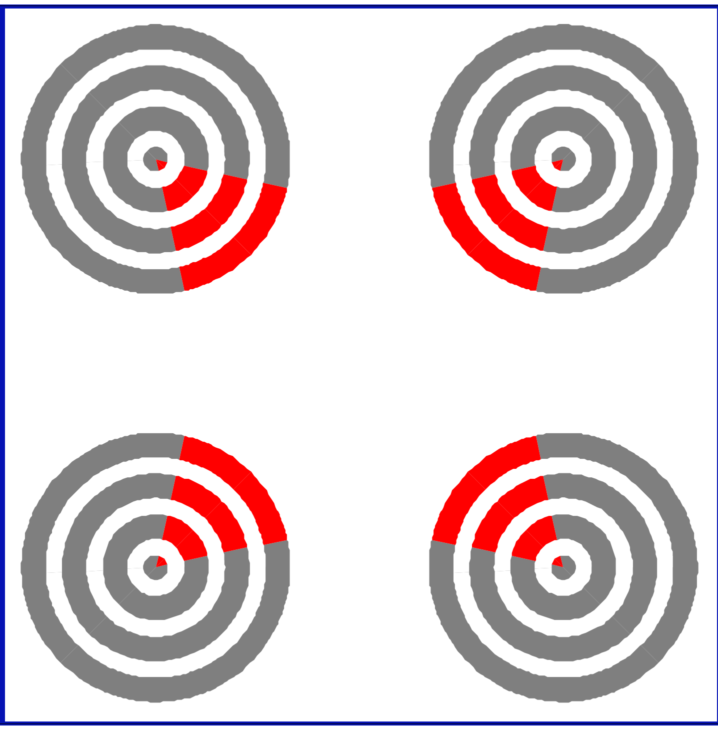
- *Another limitation*. Neural coding is a statistical population coding and, for each elementary computation, a lot of neurons are involved.
- We will not take into account explicitely this redundancy which leads to stochastic models.

A typical example : Kanizsa illusory contours

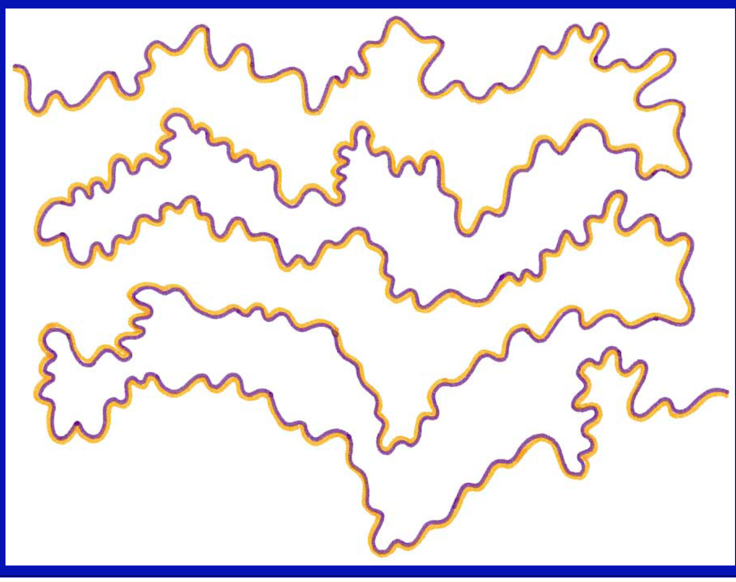
- A typical example of the problems of neurogeometry is given by well known Gestalt phenomena such as Kanizsa illusory contours.
- The visual system (V1 with some feedback from V2) constructs very long range and crisp virtual contours.



- They can even be *curved*.
- With the neon effect (watercolor illusion), virtual contours are boundaries for the diffusion of color inside them.

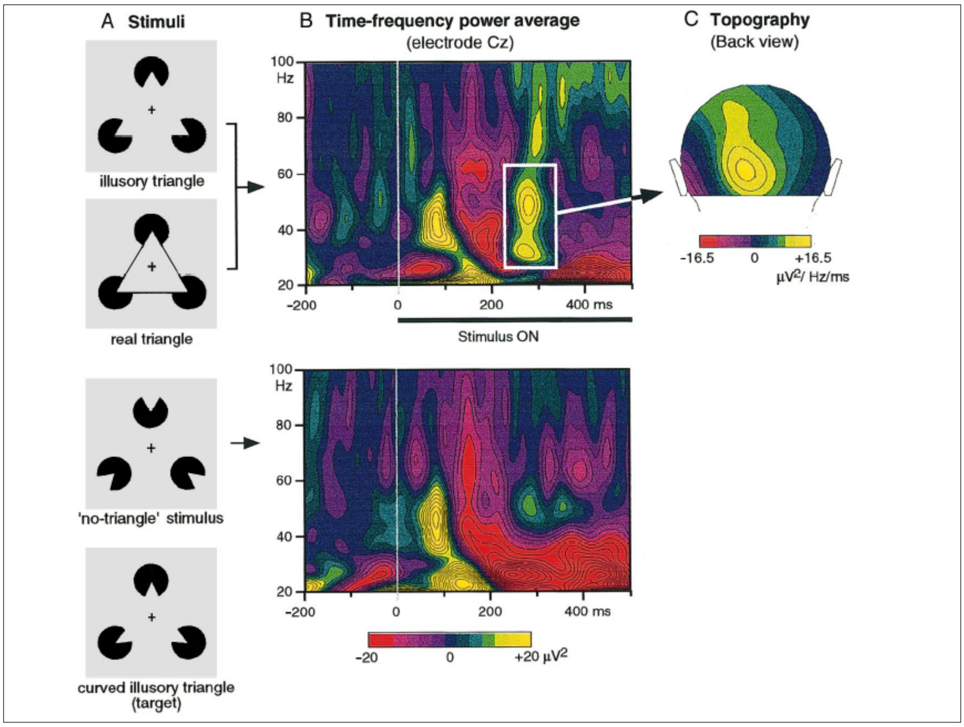


– B. Pinna, G. Brelstaff, L. Spillmann (*Vision Research*, 41, 2001)): watercolor illusion.

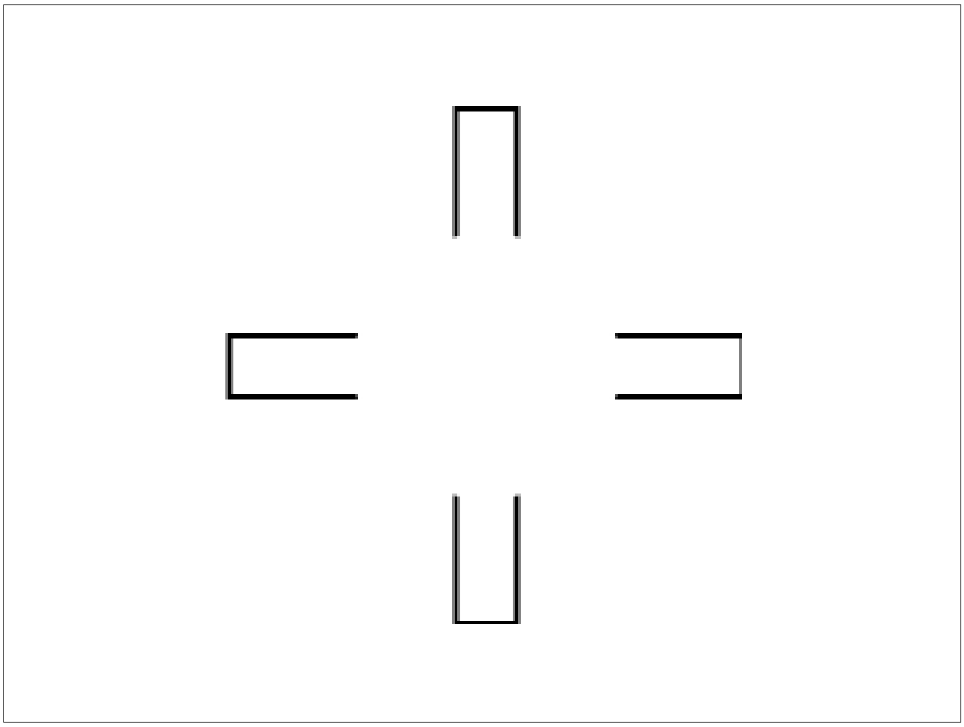


- Kanizsa subjective contours manifest a deep neurophysiological phenomenon.
- Here is a result of Catherine Tallon-Baudry in « Oscillatory gamma activity in humans and its role in object representation » (*Trends in Cognitive Science*, 3, 4, 1999).
- Subjects are presented with coherent stimuli (illusory and real triangles) « leading to a coherent percept through a bottom-up feature binding process ».

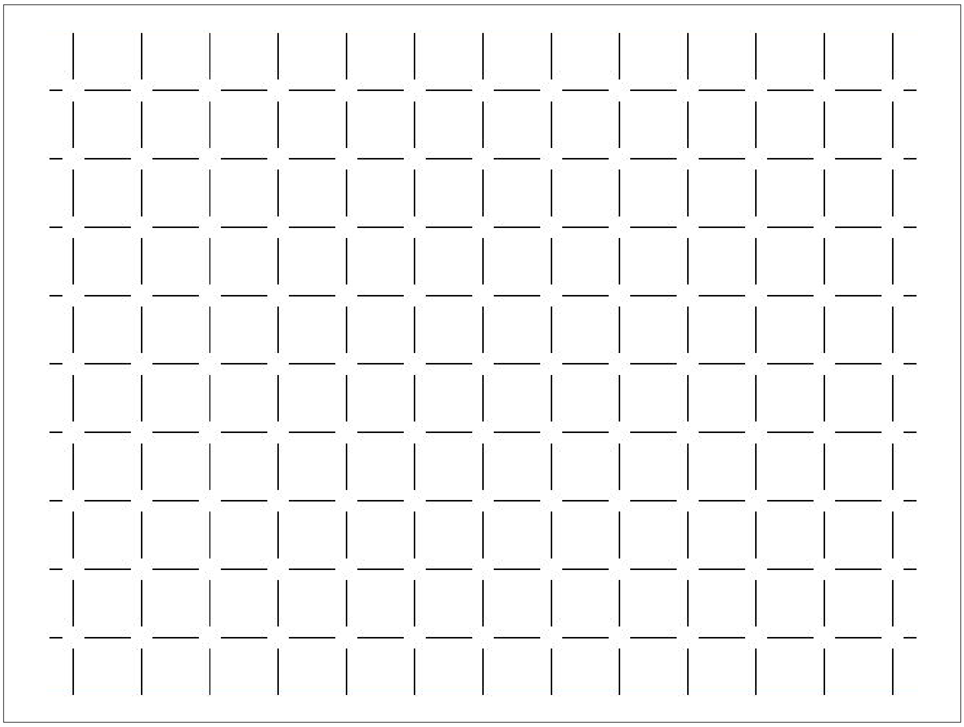
- « Time–frequency power of the EEG at electrode Cz (overall average of 8 subjects), in response to the illusory triangle (top) and to the no-triangle stimulus (bottom ».
- « Two successive bursts of oscillatory activities were observed.
  - A first burst at about 100 ms and 40 Hz. It showed no difference between stimulus types.
  - A second burst around 280 ms and 30-60 Hz. It is most prominent in response to coherent stimuli. »



- Many phenomena are striking. E.g. the change of “strategy” between a “diffusion of curvature” strategy and a “piecewise linear” strategy where the whole curvature is concentrated in a singular point.
- It is a variational problem.

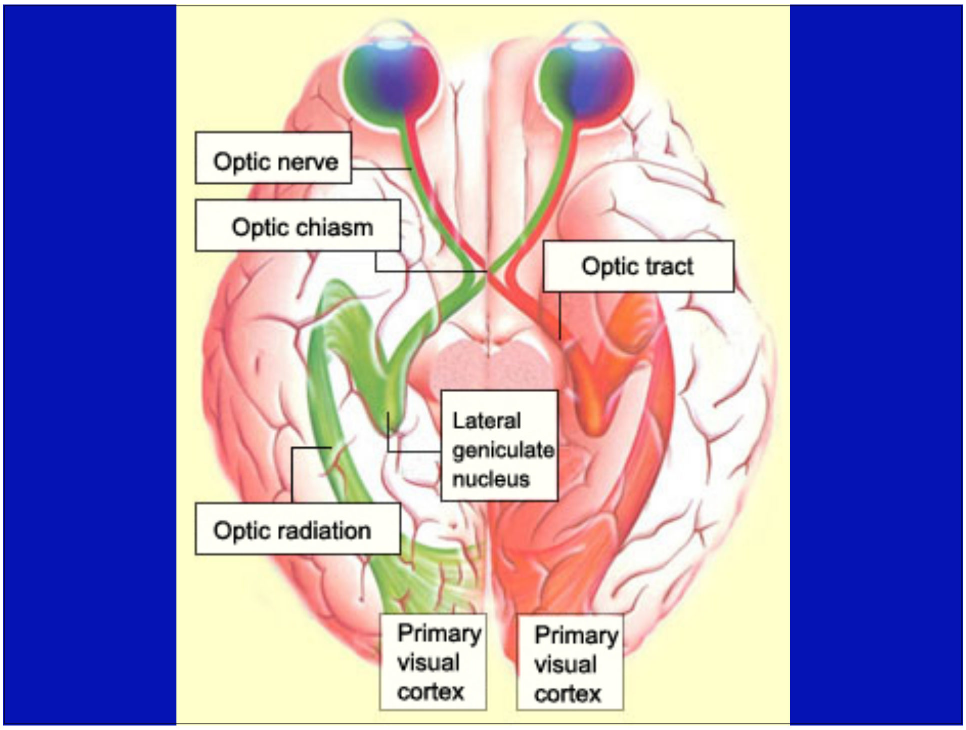


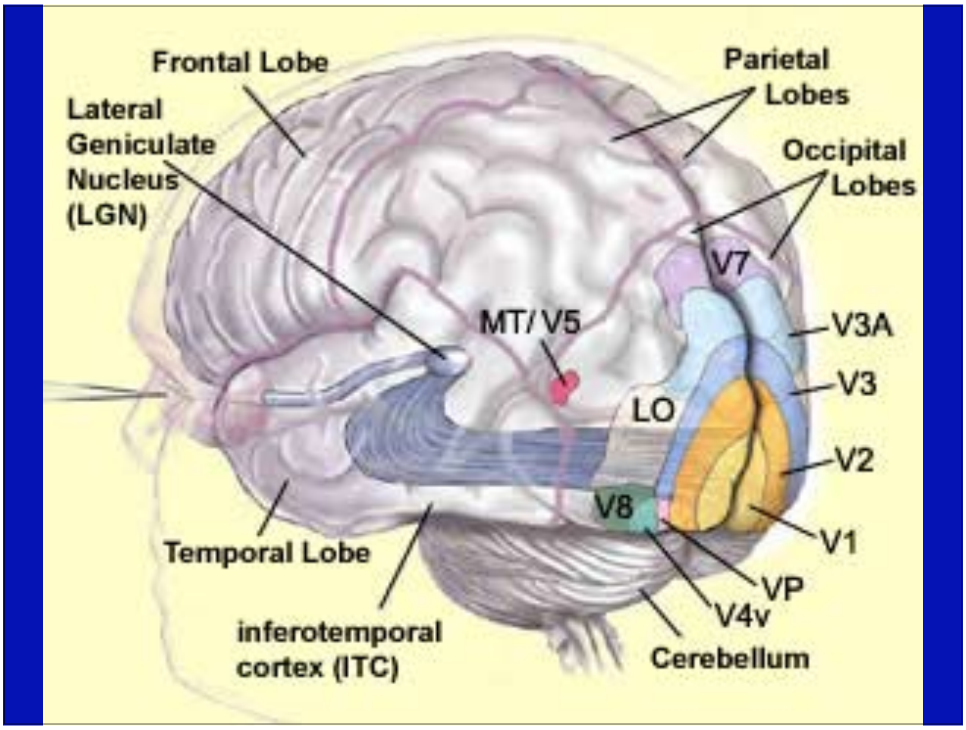
- Bistability : the illusory contour is either a circle or a square.
- The example of Ehrenstein illusion:



The primary visual cortex: area V1

- In mammals (especially higher mammals with frontal eyes), due to the optic chiasm, each visual hemifield projects onto the contralateral hemisphere.
- The fibers from nasal hemiretinae cross the optic chiasm, while the fibers from temporal hemiretinae remain on the ipsilateral side.

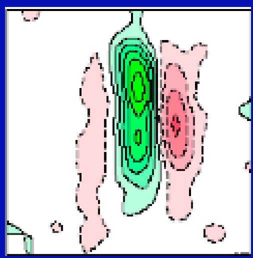

Optic nerve
Optic chiasm
Optic tract
Lateral geniculate nucleus
Optic radiation
Primary visual cortex
Primary visual cortex


Frontal Lobe
Parietal Lobes
Lateral Geniculate Nucleus (LGN)
Occipital Lobes
V7
MT/ V5
V3A
V3
LO
V2
V8
V1
Temporal Lobe
VP
V4v
inferotemporal cortex (ITC)
Cerebellum

- In the linear approximation, (simple) neurons of V1 operate as filters on the optic signal coming from the retina.
- Their receptive fields (the bundle of photoreceptors they are connected with via the retino-geniculo-cortical pathways) have receptive profiles (transfert function) with a characteristic shape.

- We look only at the simplest and most classical definition of the RFs by spiking responses (minimal discharge field).
- We don't take into account the global contextual subthreshold activity of neurons.
- We look at the simplest models.

- For simple cells, RFs are highly anisotropic and elongated along a preferential orientation.
- Level curves of the receptive profiles can be recorded :

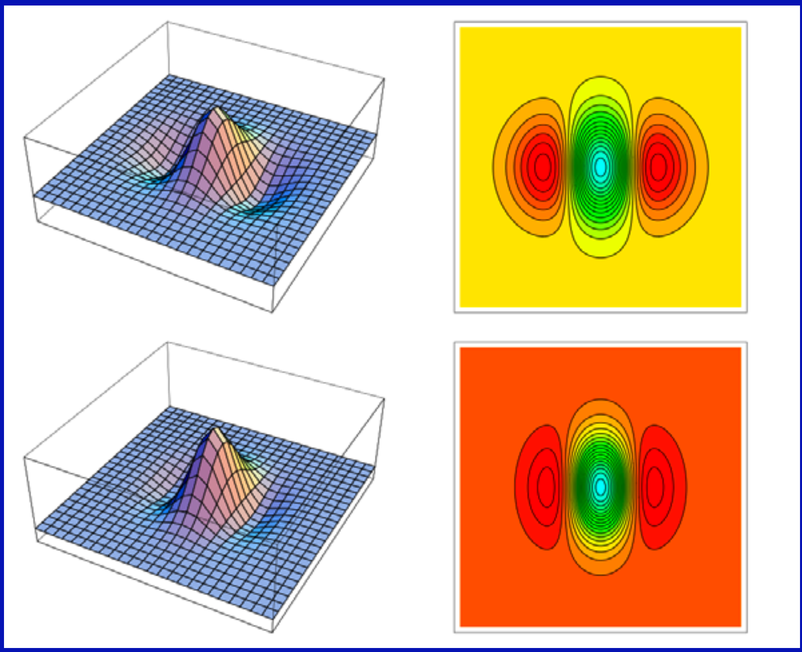


- The receptive profiles can be modeled either
  - by second order derivatives of Gaussians,
  - or by Gabor wavelets

$$\exp(i2x)\exp\left(-\left(x^2+y^2\right)\right)$$

(real part).

- Gaussian derivatives are better (see Richard Young)



- The RPs operate by convolution on the visual signal.
- Let $I(x, y)$ be the visual signal (x, y are visual coordinates on the retina).

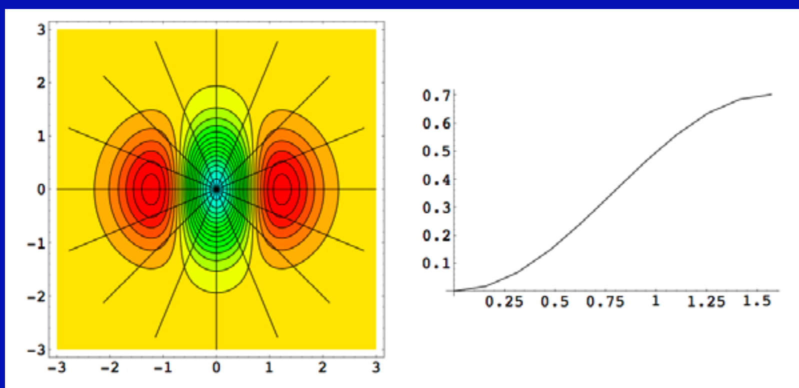
  Let $\varphi(x-x_0, y-y_0)$ be the RP of a neuron N whose RF is defined on a domain D of the retina centered on (x_0, y_0).

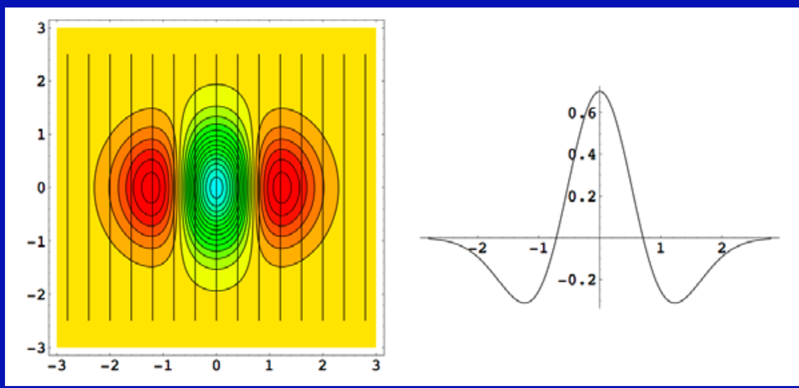
- *N* acts on the signal *I* as a filter :

$$I_\varphi(x_0, y_0) = \int_D I(x', y')\varphi(x' - x_0, y' - y_0)dx'dy'$$

- A field of such neurons act by convolution on the signal. It is a wavelet analysis.

$$I_\varphi(x, y) = \int_D I(x', y')\varphi(x' - x, y' - y)dx'dy' = (I * \varphi)(x, y)$$





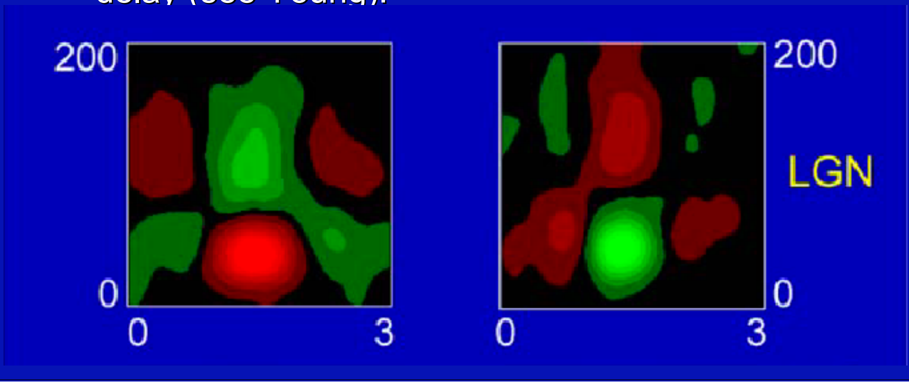
- Due to the classical formula

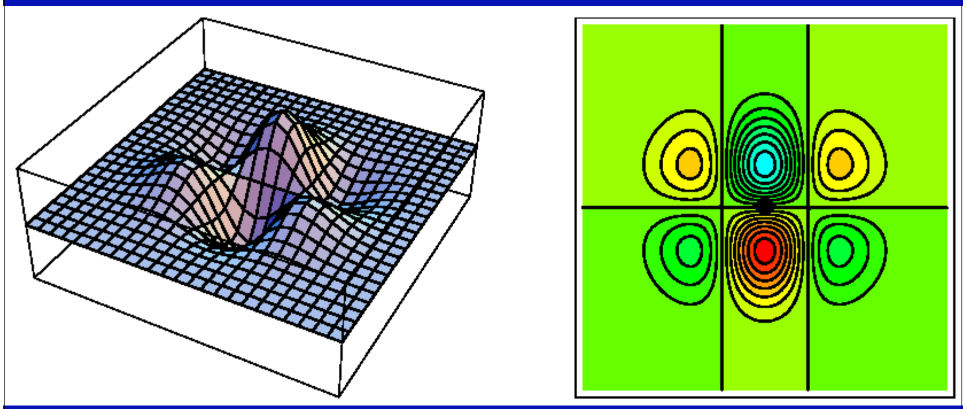
$$I{*}DG = D(I{*}G)$$

  for G a Gaussian and D a differential operator, the convolution of the signal I with a DG-shaped RF amounts to apply D to the smoothing $I{*}G$ of the signal I at the scale defined by G.

- Hence a multiscale differential geometry.

- If we add time (spatio-temporal RPs) we find even fourth order derivatives.
  - White noise method. Correlation between (i) random sequences of flashed bright / dark bars at different positions , and (ii) sequences of spikes. The time is the correlation delay (see Young).





- True RF are far more complex. They are adaped to the processing of natural images (and not bars and gratings).
- An efficient coding must reduce redundancy and maximize the mutual information between visual input and neural response.

- The statistic of natural images is very particular because there exist strong correlations between nearby RF.
- Yves Frégnac (UNIC) : 4 statistics. Drifting gratings, dense noise, natural images with eye movements, gratings with EM.
- The variability of spikes decreases with complexity and their temporal precision increases.

Hypercolumns and pinwheels

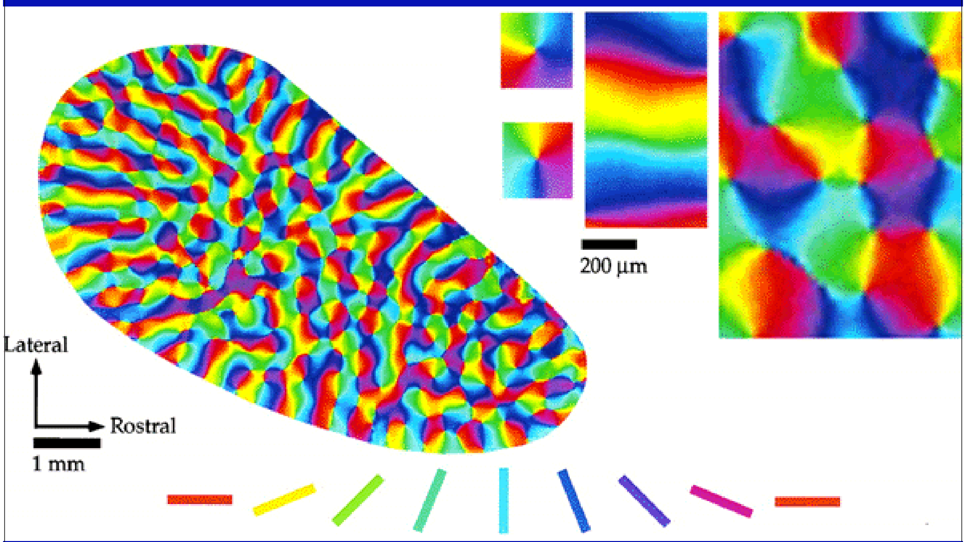
- Drastic simplification : simple cells of V1 detect a preferential orientation.
- They measure, at a certain scale, pairs (a, p) of a spatial (retinal) position a and of a local orientation p at a.

- For a given position $a = (x_0, y_0)$ in R, the simple neurons with variable orientations θ constitute an anatomically definable micromodule called an "hypercolumn".
- The hypercolumns associate retinotopically to each position a of the retina R a full exemplar P_a of the space P of orientations p at a.

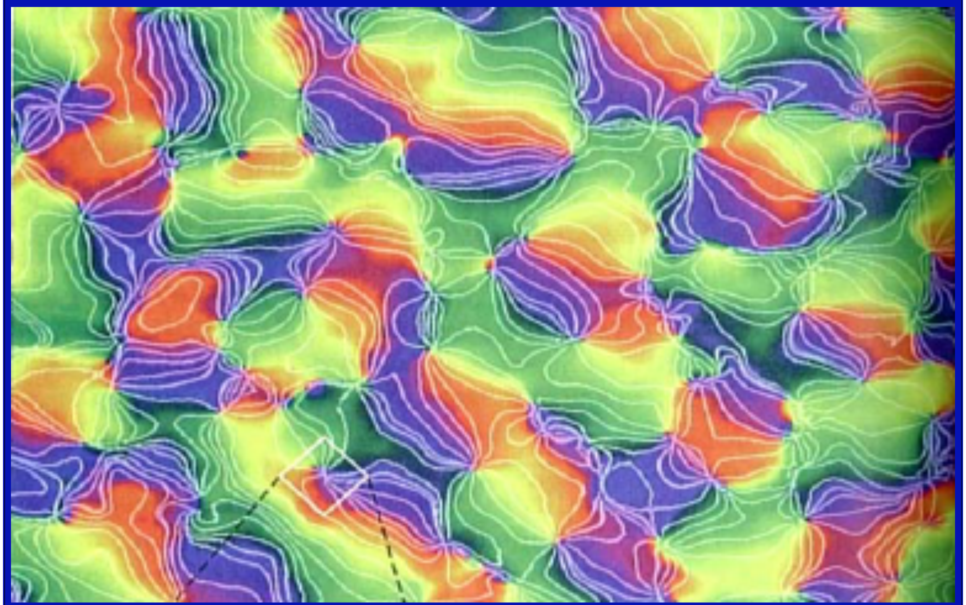
- So, this part of the functional architecture implements the fibration $\pi : R \times P \rightarrow R$ with base R, fiber P, and total space $V = R \times P$.

- Hypercolumns are geometrically organized in 2D-pinwheels.
- The cortical layer is reticulated by a network of singular points which are the centers of the pinwheels.
- Locally, around these singular points all the orientations are represented by the rays of a "wheel" and the local wheels are glued together into a global structure.

- The method (Bonhöffer & Grinvald, ~ 1990) of *in vivo optical imaging* based on activity-dependent intrinsic signals allows to acquire images of the activity of the superficial cortical layers.
- Gratings with high contrast are presented many times (20-80) with e.g. a width of 6.25° for the dark strips and of 1.25° for the light ones, a velocity of 22.5°/s, different (8) orientations.



- There are 2 classes of points :
  - regular points where the orientation field is locally trivial;
  - singular points at the center of the pinwheels;
- Two adjacent singular points are of opposed chirality.



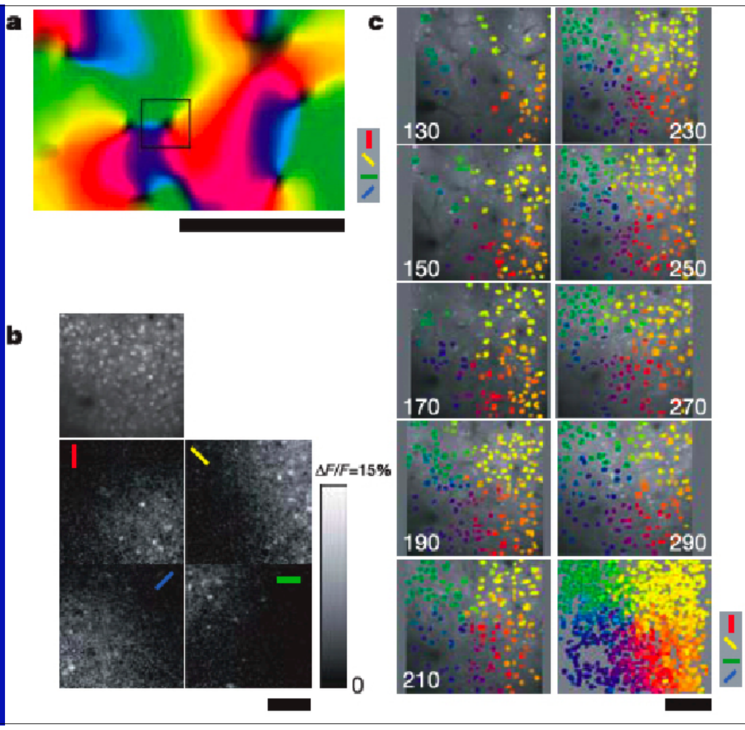
- What is the structure near singularities ?
- The spatial (50μ) and depth resolutions of optical imaging is not sufficient.
- One needs single neuron resolution to understand the micro-structure.

- Two-photon calcium imaging *in vivo* (confocal biphotonic microscopy) provides functional maps at single-cell resolution.
  - Kenichi Ohki, Sooyoung Chung, Prakash Kara, Mark Hübener, Tobias Bonhoeffer and R. Clay Reid:

    Highly ordered arrangement of single neurons in orientation pinwheels, Nature, 442, 925-928 (24 August 2006) .

- (In cat) pinwheels are higly ordered at the micro level and « thus pinwheels centres truly represent singularities in the cortical map ».
- Injection of calcium indicator dye (Oregon Green BAPTA-1 acetoxylmethyl esther) which labels few thousands of neurons in a 300-600μ region.
- Two-photon calcium imaging measures simultaneously calcium signals evoked by visual stimuli on hundreds of such neurons at different depths (from 130 to 290μ by 20μ steps).

- One finds pinwheels with the same orientation wheel.
- « This demonstrates the columnar structure of the orientation map at a very fine spatial scale ».

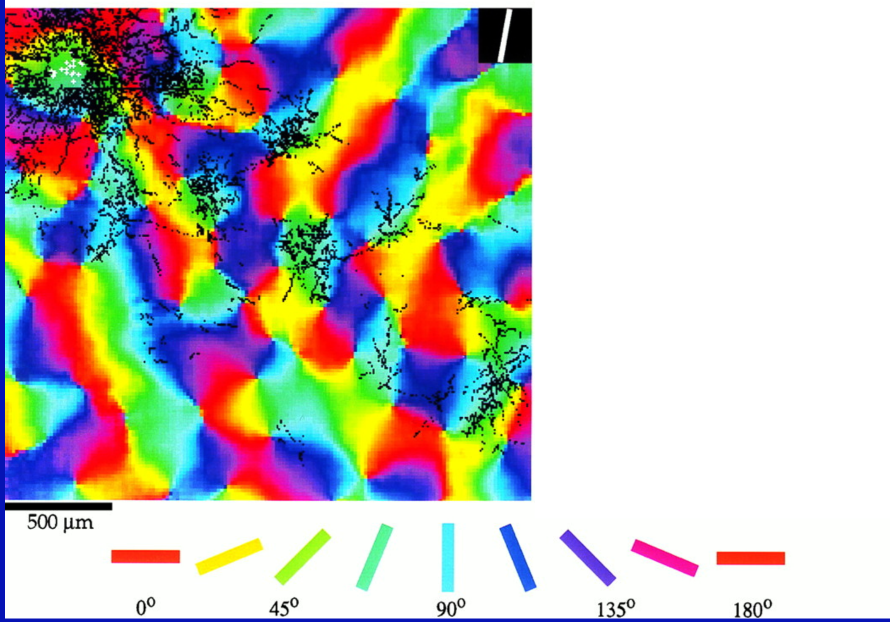


The horizontal structure

- The "vertical" retinotopic structure is not sufficient. To implement a global coherence, the visual system must be able to compare two retinotopically neighboring fibers P_a et P_b over two neighboring points a and b.
- This is a problem of parallel transport. It has been found at the empirical level by the discovery of "horizontal" cortico-cortical connections.

- Cortico-cortical connections are slow (≈ 0.2m/s) and weak.
- They connect neurons of almost similar orientation in neighboring hypercolumns.
- This means that the system is able to know, for b near a, if the orientation q at b is the same as the orientation p at a.

- The next slide shows how a marker (biocytin) injected locally in a zone of specific orientation (green-blue) diffuses via horizontal cortico-cortical connections.
- The key fact is that the long range diffusion is highly anisotropic and restricted to zones of the same orientation (the same color) as the initial one.



- Moreover cortico-cortical connections connect neurons coding pairs (a, p) and (b, p) such that p is approximatively the orientation of the axis ab (William Bosking).
  - « The system of long-range horizontal connections can be summarized as preferentially linking neurons with co-oriented, co-axially aligned receptive fields ».
- So, the well known Gestalt law of “good continuation” is neurally implemented.

- In fact, a certain amount of curvature is allowed in alignements.
- These experimental results mean essentially that the contact structure of the fibration $\pi : V = R \times P \rightarrow R$ is neurally implemented.

The contact structure of V1

- The first model : the space of 1-jets of curves C in R.
- It is the beginning of neurogeometry (Hoffman, Koenderink).

- If C is curve in R (a contour), it can be lifted to V. The lifting Γ is the map (1-jet)

$$j : C \to \quad V = R \times P$$

wich associates to every point a of C the pair

(a, p_a) where p_a is the tangent of C at a.

- This Legendrian lift Γ represents C as the enveloppe of its tangents (projective duality).
- In terms of local coordinates (x, y, p) in V, the equation of Γ writes $(x, y, p) = (x, y, y')$.

- If we have an image $I(x, y)$ on R, we can lift it in V by lifting its level curves.

Fonctionality of jet spaces

- The functional interest of jet spaces is that they can be implemented by “point processors” (Koenderink) such as neurons.
- But then a functional architecture is needed.
- Functional architectures of point processors can compute features of differential geometry.

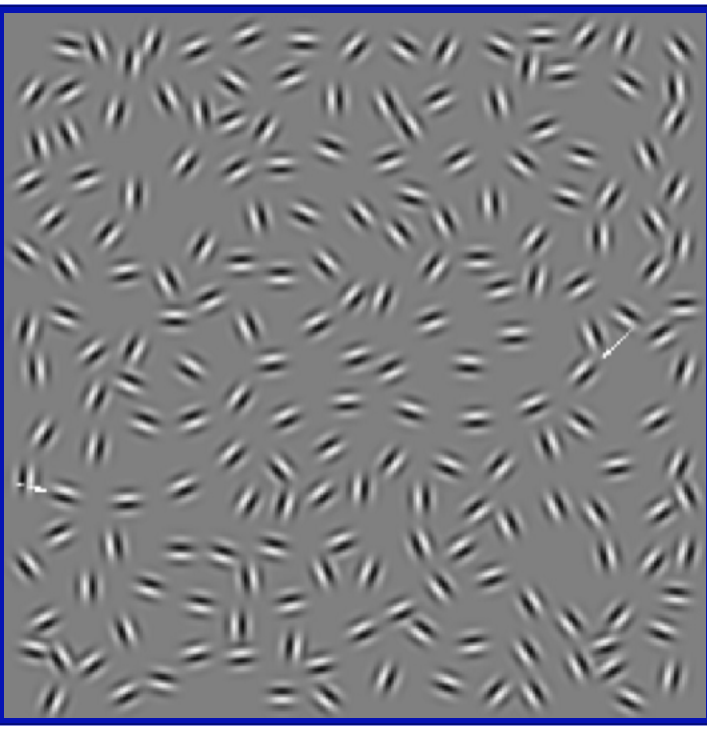
- The key idea is
  - (1) to add new independent variables describing local features such as orientation.
  - (2) to introduce an integrability constraint to integrate them into global structures.
- Neuro-physiologically, this means to add feature detectors and to couple them via a functional architecture in order to ensure binding.

- To every curve C in R is associated a curve Γ in V. But the converse is of course false.
- If $\Gamma = (a, p) = (x, y(x), p(x))$ is a curve in V, the projection $a = (x, y(x))$ of Γ is a curve C in R. But Γ is the lifting of C iff $p(x) = y'(x)$.
- This condition is called a Frobenius integrability condition. It says that to be a coherent curve in V, Γ must be an integral curve of the contact structure of the fibration π.

Frobenius condition and Association field

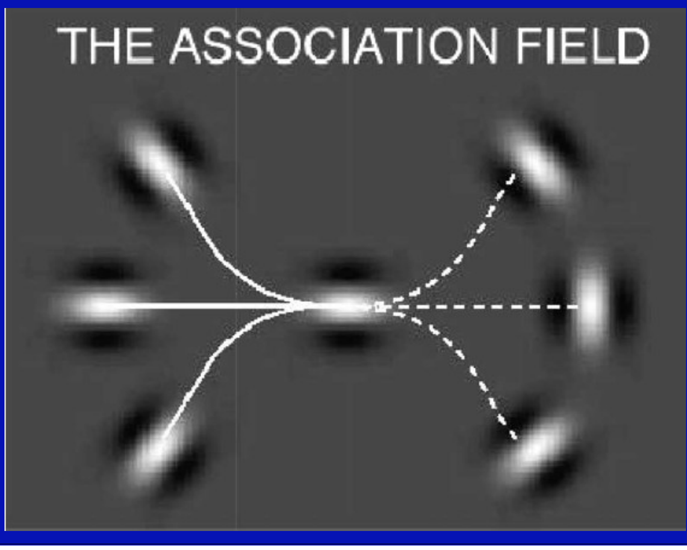
- Frobenius integrability condition corresponds to the psychophysical experiments on the association field (David Field, Anthony Hayes and Robert Hess).
- They explain experiments on good continuation : pop out of a global curve against a background of randomly distributed distractors

- Let (a_i, p_i) be a set of segments embedded in a background of randomly distributed distractors. The segments generate a perceptively salient curve (pop-out) iff the p_i are tangent to the curve C optimally interpolating between the a_i.

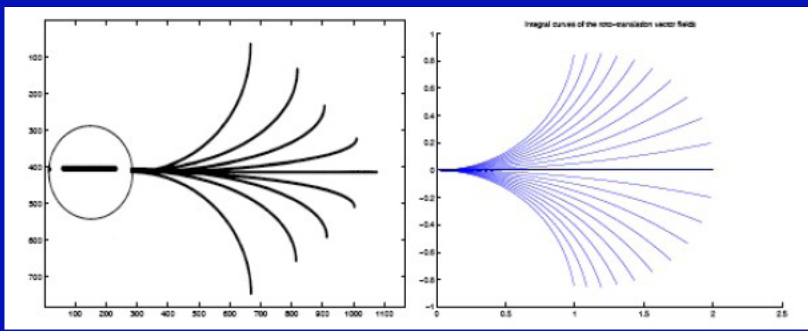


- This is a discretized version of the integrability condition.
- The integrability induces a binding of the local elements. The activities of the neurons detecting them are synchronized and the synchronization produces the pop out.

- One must have the following type of horizontal connectivity :



- But this is exactly the integrability condition : the association field (left) correspond to the simplest integral curves of the contact distribution (right).



- Frobenius condition is extremely simple :

$$p = dy/dx$$

- But it contains deep mathematics.

- Frobenius integrability condition is equivalent to the fact that if

$$t = (x, y, p; 1, y', p')$$

is a tangent vector to V at the point

(x, y, p), then t is in the kernel of the 1-form

$$\omega = dy - pdx$$

($\omega = 0$ means $p = dy / dx$).

- $\omega(1, y', p') = dy(1, y', p') - pdx(1, y', p')$

$= y' - p$

- To compute the value of a 1-form ω on a tangent vector $t = (\xi, \eta, \pi)$ at (x, y, p), one applies the rules

$$dx(t) = \xi, \; dy(t) = \eta, \; dp(t) = \pi.$$

- So the kernel of the 1-form ω is the field of the planes (called the contact planes)

$$\eta - p\xi = 0 .$$

- $X_1 = \partial_x + p\partial_y = (\xi = 1, \eta = p, \pi = 0)$, and $X_2 = \partial_p = (\xi = 0, \eta = 0, \pi = 1)$ are evident generators.

- Moreover, in a Legendrian lift Γ, the vertical component p' of a tangent vector is the curvature of the curve C in the base space R :

$$p = y' \Rightarrow p' = y''$$

- The field of the contact planes has many integral curves : all the Legendrian lifts. But it has no integral surfaces.
- This is due to the fact that the contact planes "rotate" too fast to be the tangent planes of a surface.