Université de La Rochelle
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Neuromathematical Models of Vision

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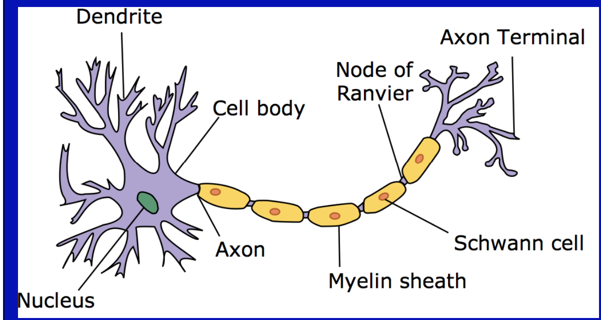
CAMS, EHESS

- Four examples :

1. Spikes and differential equations.
2. Receptive profiles and wavelet analysis.
3. Pinwheels and phase fields.
4. Horizontal cortico-cortical connections and sub-Riemannian geometry.

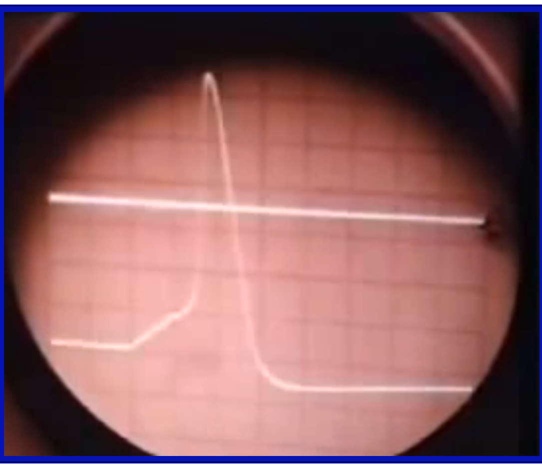
Neurons, spikes, and HH



- The activity of a neuron is essentially an emission of spikes (action potential) along its axon.
- Spikes are strong and fast variations of the membrane potential *V* defined by the concentrations of ions between the inside and the outside of the neuron.
- The main ions are Na^+, K^+, and also Ca^{++}, Cl^- .

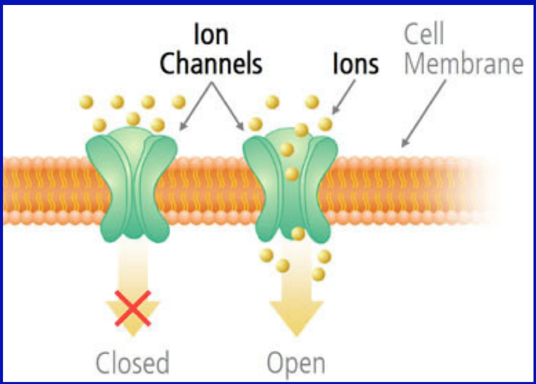
- In the resting state of the membrane, *in* is – w.r.t. *out* because the K^+ ions can easily cross the membrane while the Na^+ ions are more constrained.
- The dynamics of Na^+, K^+, Ca^{++}, Cl^- ions across the ionic channels of the membrane defines a rest potential (RP) $V \approx -75/70$ mV.
- K^+ is dominant *in* and Na^+ is dominant *out*.

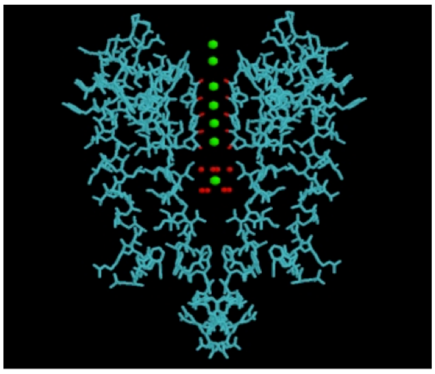
- Phenomenology of spikes :
  - existence of a stable equilibrium,
  - existence of a threshold for spike triggering,
  - fast emission (exponential growth),
  - slow return to equilibrium.



- The ion dynamics is twofold:
  - diffusion along concentration gradients,
  - flow due to a difference of electrical potential.
- The balance between these two opposite dynamics defines the equilibrium potential (EP):
  - $Na^+ = +62$ mV,
  - $K^+ = -80$ mV,
  - $Ca^{++} = +123$ mV,
  - $Cl^- = -65$ mV.

- Fondamental role of ion channels.

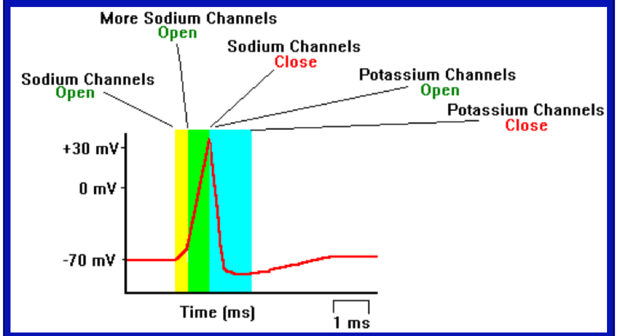




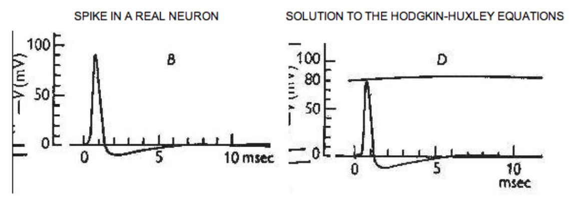
A potassium channel/David S. Goodsell,The Scripps Research Institute

- The membrane is initially polarized.
- A depolarization increases RP. When it crosses the threshold of – 55/45 mV the neuron “fires” and emits a spike (action potential, "explosive" depolarization) which propagates along the axon.
- There is a positive feedback of depolarization on the (fast) aperture of Na^+ channels and RP increases catastrophically up to + 60 mV (≈ EP of Na^+).
- Afterwards, Na^+ channels are inactivated.

- But the strong depolarization opens the (slow) K^+ channels, the K^+ ions flow out, and the membrane is *repolarized* and returns "*slowly*" to the RP after a period of *hyperpolarization* (– 85 mV ≈ EP of K^+) .
- The recovery period is followed by a refractory period.



- Remarkable non-linear equations of Hodgkin & Huxley (1952, Nobel Prize 1963).
- Giant axon of the squid.



Figures from Hodgkin and Huxley, *A quantitative description of membrane current and its application to conduction and excitation in nerve*, The Physiological Society, volume 117, 1952; Wiley-Blackwell Publishing.

$$\begin{cases} C\dot{V} = I - \overline{g_{Na}}m^3h\,(V - V_{Na}) - \overline{g_K}n^4\,(V - V_K) - \overline{g_l}\,(V - V_l) \\ \dot{m} = \frac{m_\infty(V) - m}{\tau_m(V)} \\ \dot{h} = \frac{h_\infty(V) - h}{\tau_h(V)} \\ \dot{n} = \frac{n_\infty(V) - n}{\tau_n(V)}\ . \end{cases}$$

V = membrane potential
m = fast activation of the Na^+ ionic current
h = slow inactivation of the Na^+ ionic current
$m^3h \in [0,1]$ = proportion of opened Na^+ channels
n = activation of the K^+ ionic current
n^4 = proportion of opened K^+ channels
I = external current

$\overline{g_{Na}}, \overline{g_K}, \overline{g_l}$ = maximal conductances/surface unit for the Na^+ and K^+ ionic currents and the leakage current
$V_{Na}, V_K = Na^+, K^+$ Nernst potentials
C = membrane capacity/surface unit.

- So V is the main variable and m, n, h are "gating" variables (membrane permeability).

Functions $m_\infty(V)$, $h_\infty(V)$, $n_\infty(V)$ and characteristic times $\tau_m(V)$, $\tau_h(V)$ and $\tau_n(V)$ have the form
$\frac{\alpha}{\alpha+\beta}$ and $\frac{1}{\alpha+\beta}$
with α and β functions of V of type $\frac{A}{1\pm e^B}$ or $\frac{1}{e^B}$ with A and B linear.

The first equation for $C\dot{V}$ expresses the conservation of the electric charge of the membrane.

Equations for $\dot{m}$, $\dot{h}$ and $\dot{n}$ express the velocities of channels opening/closure.

They depend upon gates whose number gives the exponents of m, n and h in the equations.

- To integrate a *system* of such equations (neural nets) they must be simplified.
- Example : 2D model.
- They cannot model a slow return to equilibrium (3D are needed : Zeeman 1972).
- But they can model trains of spikes using hysteresis cycles.

"Instantaneous" Na^+ activation.

$g_{Na} = \overline{g_{Na}} m_\infty(V)$ with $m_\infty(V)$ function of V.

K^+ channels of type $\overline{g_K} n$.

$C = 1$, $I = 10$,

$V_l = -80$, $\overline{g_l} = 8$, $V_{Na} = 60$, $\overline{g_{Na}} = 20$, $V_K = -90$, $\overline{g_K} = 10$,

$m_\infty(V) = \left(1 + \exp\left(\frac{-20-V}{15}\right)\right)^{-1}$,

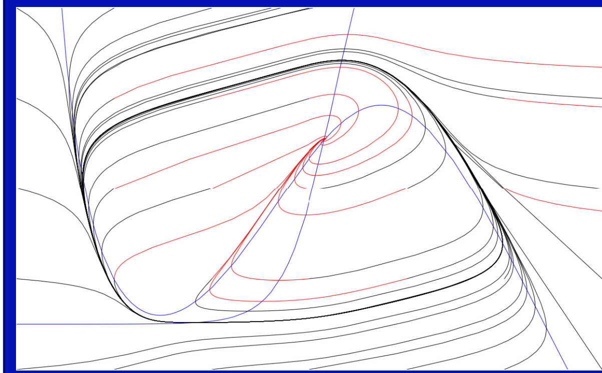
$n_\infty(V) = \left(1 + \exp\left(\frac{-25-V}{5}\right)\right)^{-1}$,

$\tau_n(V) = 1$.

V varies between -90 and 30, n varies between -0.1 and 0.7.

$$\begin{cases} \dot{V} = 10 - 20\frac{V-60}{1+\exp\left(-\frac{V+20}{15}\right)} - 10n\,(V+90) - 8\,(V+80) \\ \dot{n} = -n + \frac{1}{1+\exp\left(-\frac{V+25}{5}\right)}\,. \end{cases}$$

- Non linear equations.
- Trajectories in the (V, n) plane
  - (black = forward, red = backward, blue = nullclines).



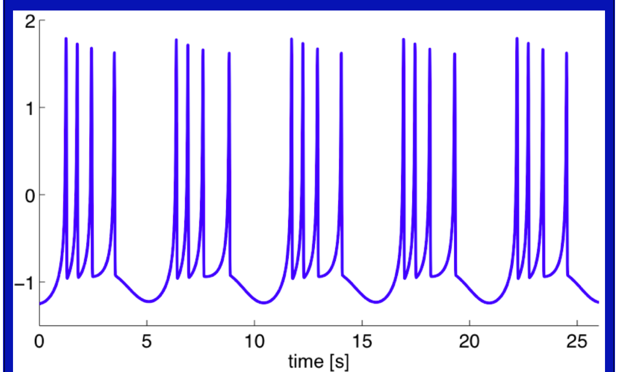
The slow manifold Σ, is the nullcline $\dot{V} = 0$ and has the form of a cubic.

Two stable branches separated by an unstable branch.

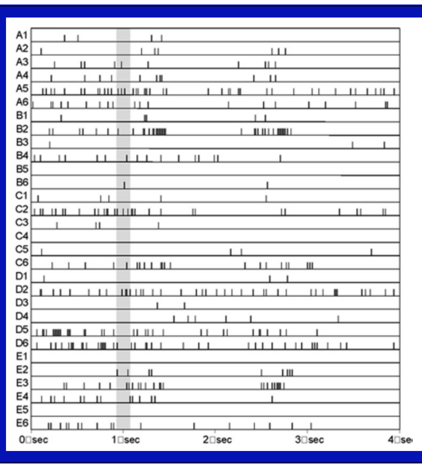
Unstable equilibrium at the intersection of Σ with the nullcline $\dot{n} = 0$ of n.

Stable limit cycle along the stable branches of Σ.

- Complex dynamics : trains, bursts, etc.

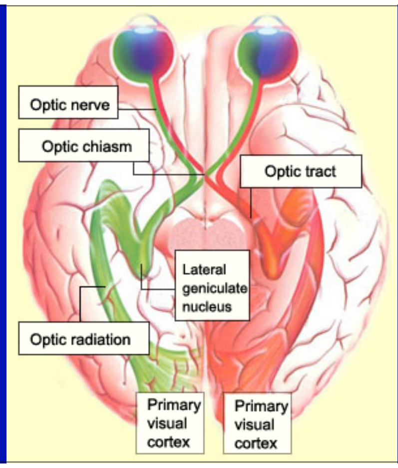


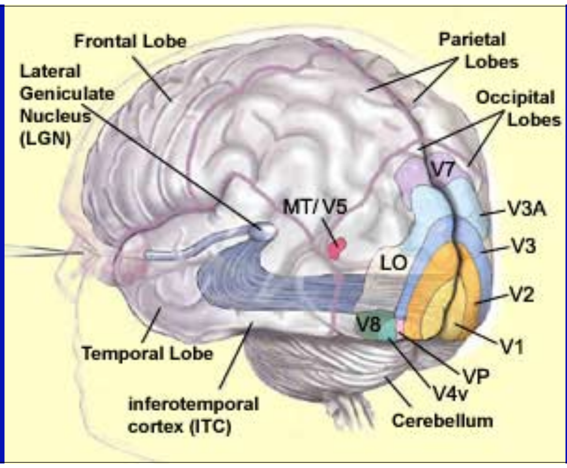
- Neural coding.
- Spike trains of 30 neurons of a monkey's V1.
- Gray strip = 150ms (typical time for a fast brain computation) .
- Simplest hypothesis : a spike frequency codes for a numerical value.



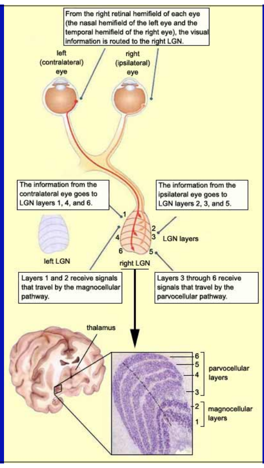
Receptive profiles and wavelet analysis

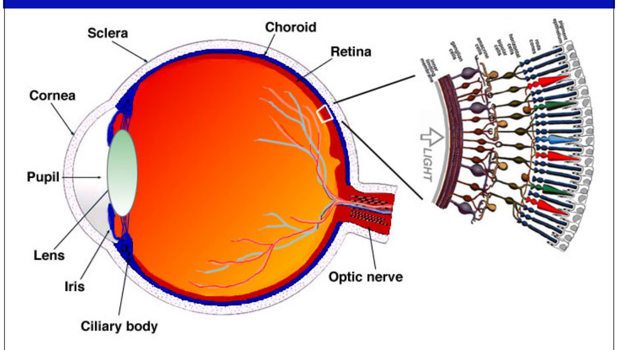
- The visual brain:
  - Retina,
  - Lateral geniculate nucleus,
  - Primary visual cortex.

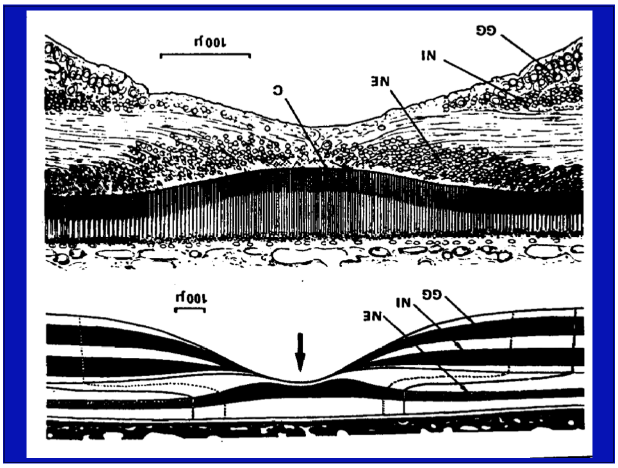


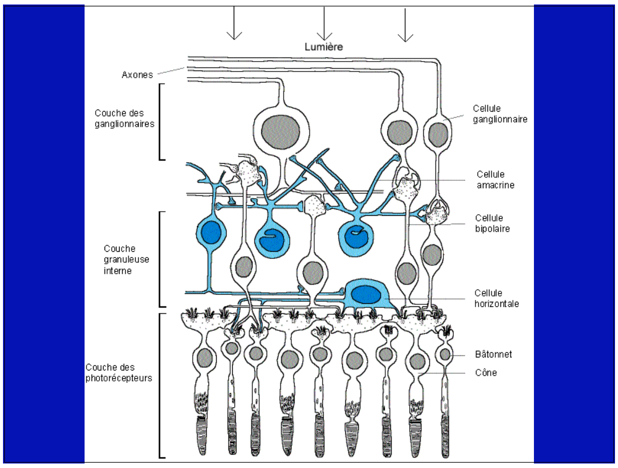


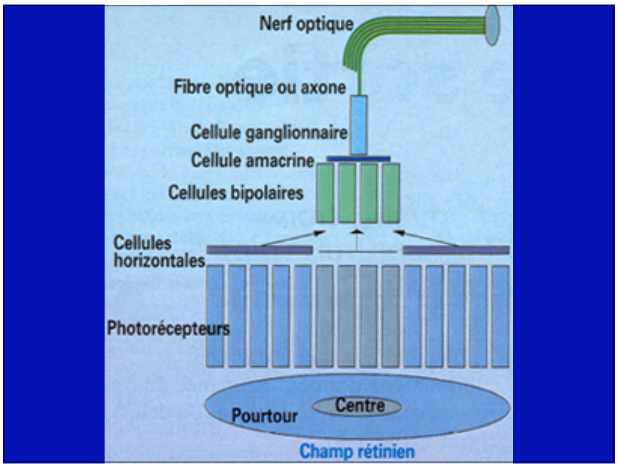
Parvo (X)	**Magno** (Y)
Toniques	Phasiques
Petite taille	Grande taille
Axones fins	Axones larges
Vitesse de conduction lente	Vitesse de conduction rapide
Centre étroit, gradient centre/périphérie fort	Centre large, gradient centre/périph faible
Résolution spatiale elevée, résolution temporelle faible	Résolution spatiale faible, résolution temporelle élevée
Analyseur de contrastes spatiaux (formes)	Détection de mouvements (analyse temporelle)
Calcul de $\Delta G{\cdot}I$	Calcul de $\partial(\Delta G{\cdot}I) / \partial t$
Sommation linéaire	Sommation non linéaire

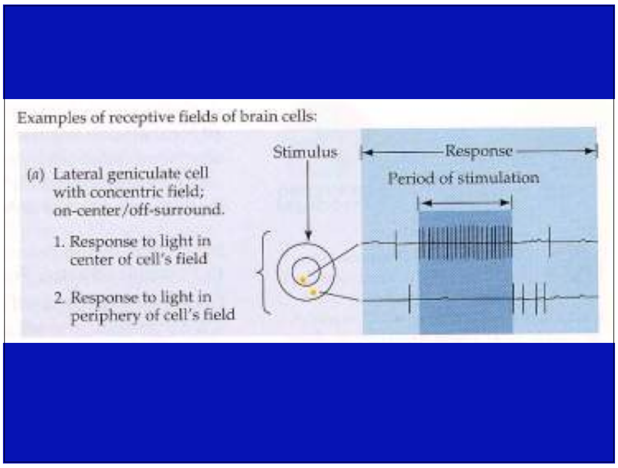


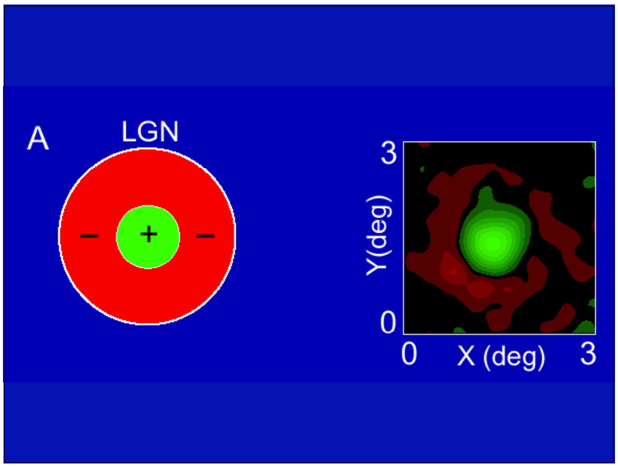


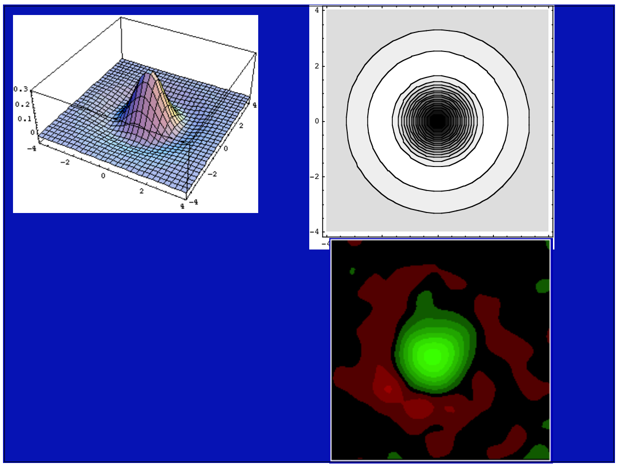



Lumière
Axones
Couche des ganglionnaires
Cellule ganglionnaire
Cellule amacrine
Cellule bipolaire
Couche granuleuse interne
Cellule horizontale
Couche des photorécepteurs
Bâtonnet
Cône


Nerf optique
Fibre optique ou axone
Cellule ganglionnaire
Cellule amacrine
Cellules bipolaires
Cellules horizontales
Photorécepteurs
Pourtour
Centre
Champ rétinien


Examples of receptive fields of brain cells:
Stimulus
Response
Period of stimulation
(a) Lateral geniculate cell with concentric field; on-center/off-surround.
1. Response to light in center of cell's field
2. Response to light in periphery of cell's field





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

  Let $\varphi(x\text{-}x_0, y\text{-}y_0)$ 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.

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

- But from 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 which is a wavelet analysis.

Wavelet analysis

- Signals $f \in L^2(\mathbb{R})$
- Fourier transform (analysis).

$$\widehat{f}(\omega) = \frac{1}{\sqrt{2\pi}} \int_{\mathbb{R}} f(x) e^{-i\omega x} dx = \left\langle f(x) \middle| e^{i\omega x} \right\rangle$$

- Inverse transform (synthesis).

$$f(x) = \frac{1}{\sqrt{2\pi}} \int_{\mathbb{R}} \widehat{f}(\omega) e^{i\omega x} d\omega = \left\langle \widehat{f}(\omega) \middle| e^{-i\omega x} \right\rangle$$

- Isometry.
- Geometrical information is delocalized.

- Gabor transform (analysis).

$$Gf(\omega, u) = \frac{1}{\sqrt{2\pi}} \int_{\mathbb{R}} f(x) g(x-u) e^{-i\omega x} dx = \langle f(x) \, | g_{\omega,u}(x) \rangle$$

- Inverse transform (synthesis).

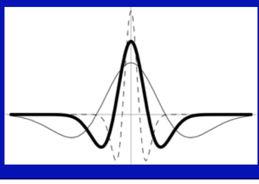
$$f(x) = \frac{1}{2\pi} \int_{\mathbb{R}^2} Gf(\omega, u) g(x-u) e^{i\omega x} d\omega du$$

- Isometry.
- Geometrical information is localized, but only at one scale.

- Multiscale wavelet transform (analysis).
- Mother wavelet and scaling :

$$\psi_s(x) = \frac{1}{\sqrt{s}}\psi\left(\frac{x}{s}\right)$$

- Typical example : ΔG



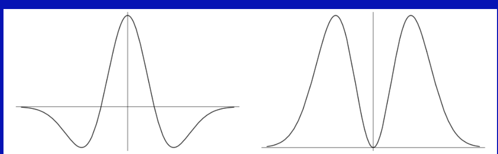
- Direct wavelet transform :

$$Wf(s,u) = \int_{\mathbb{R}} f(x)\psi_s(x-u)dx = \langle f(x)\,|\psi_{s,u}(x)\rangle$$

- $$(C) : \widehat{\psi}(0) = 0 \quad \text{et} \quad C_\psi = \int_{\mathbb{R}+} \frac{\left|\widehat{\psi}(\omega)\right|^2}{\omega} d\omega < \infty$$

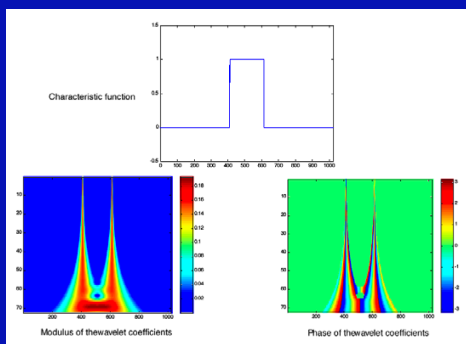
$$\psi(x) = \left(1-x^2\right)e^{-\frac{x^2}{2}} \qquad \widehat{\psi} = \omega^2 e^{-\frac{\omega^2}{2}}$$

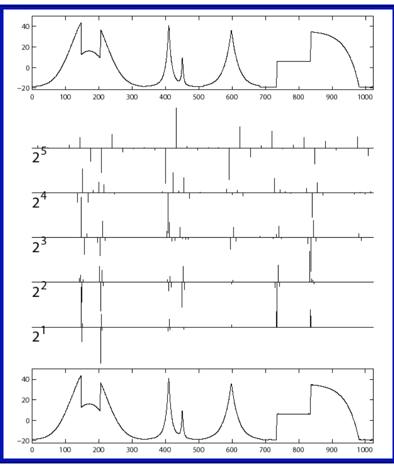
$$C_\psi = \int_{\mathbb{R}+} \frac{|\widehat{\psi}(\omega)|^2}{\omega} d\omega \qquad C_\psi = \int_{\mathbb{R}+} \omega^3 e^{-\omega^2} d\omega = \frac{1}{2}$$

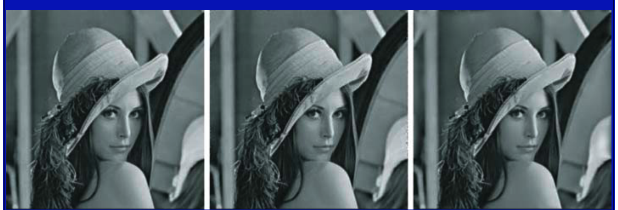


- $$f(x) = \frac{1}{C_\psi}\int_{\mathbb{R}+}\int_{\mathbb{R}} Wf(s,u)\psi_s(x-u)dsdu$$

- Extraction of singularities :

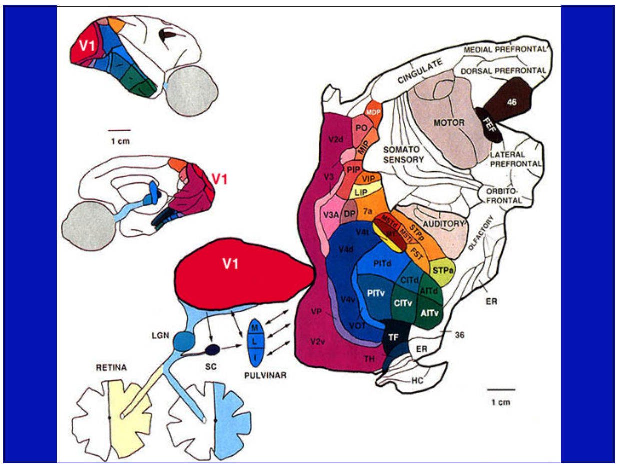


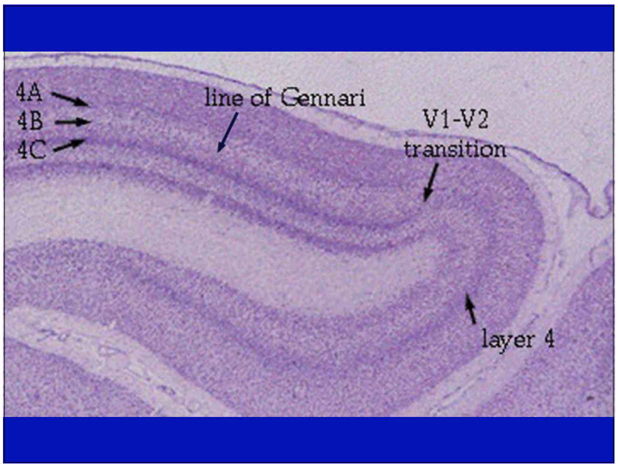


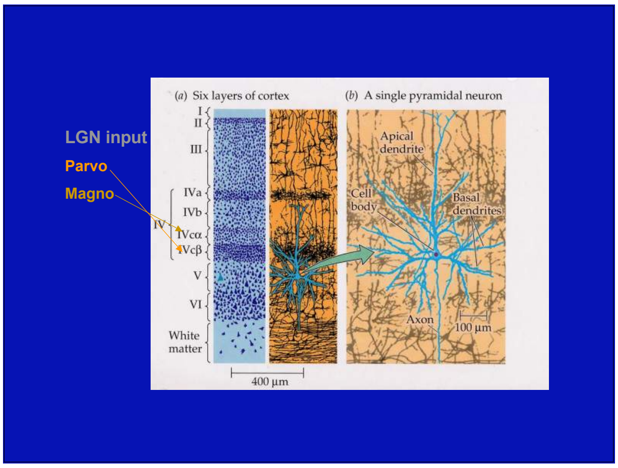


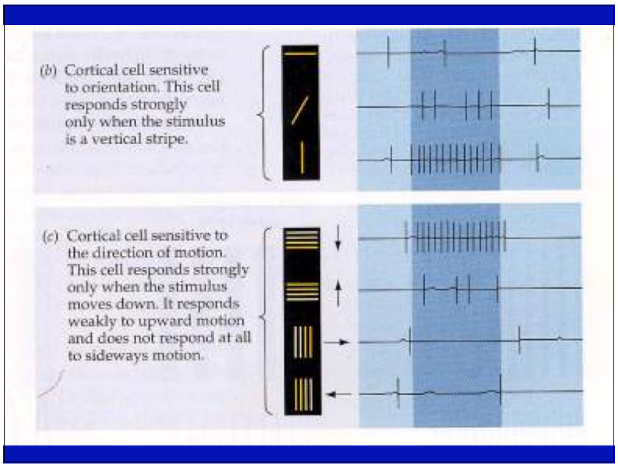
The primary visual cortex: area V1

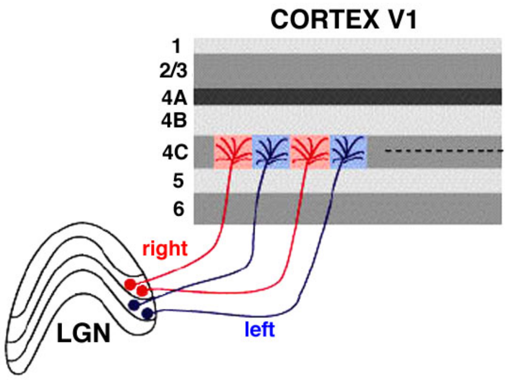
- In mammals (especially higher mammals with frontal eyes), due to the optic chiasm, each visual hemifield projects onto the contralateral hemisphere.
- The fibers from nasal hemiretinae cross the optic chiasm, while the fibers from temporal hemiretinae remain on the ipsilateral side.

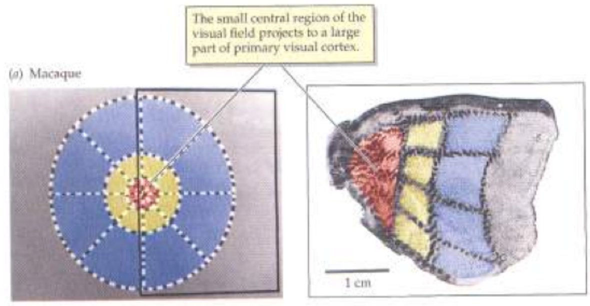

V1
1 cm
V1
V1
LGN
SC
PULVINAR
RETINA
CINGULATE
MEDIAL PREFRONTAL
DORSAL PREFRONTAL
46
MOTOR
FEF
SOMATO SENSORY
LATERAL PREFRONTAL
ORBITO-FRONTAL
AUDITORY
OLFACTORY
V2d
PO
MDP
MIP
PIP
V3
VIP
LIP
V3A
DP
7a
V4t
V4d
STPp
FST
STPa
PITd
CITd
AITd
PITv
CITv
AITv
V4v
VOT
VP
V2v
TF
TH
ER
36
HC
1 cm


4A
4B
4C
line of Gennari
V1-V2 transition
layer 4

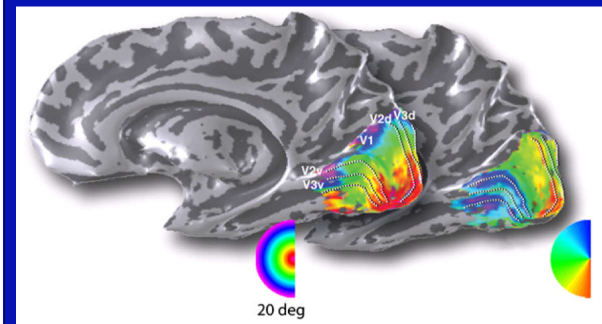

LGN input
Parvo
Magno
(a) Six layers of cortex
(b) A single pyramidal neuron
I
II
III
IVa
IVb
IV
IVcα
IVcβ
V
VI
White matter
400 μm
Apical dendrite
Cell body
Basal dendrites
Axon
100 μm


(b) Cortical cell sensitive to orientation. This cell responds strongly only when the stimulus is a vertical stripe.
(c) Cortical cell sensitive to the direction of motion. This cell responds strongly only when the stimulus moves down. It responds weakly to upward motion and does not respond at all to sideways motion.





- fMRI image of the retinotopic projection of a visual hemifield onto its visual cortical hemisphere
- Concentric circles and rays are coded by colors.

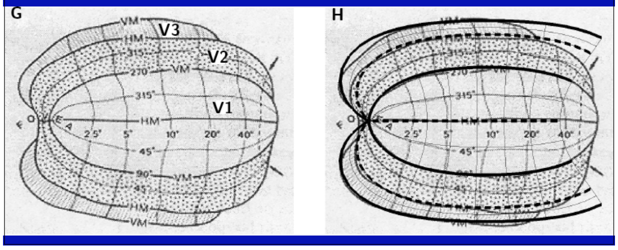


- A good model is a wedge-dipole model for V1, V2, and V3

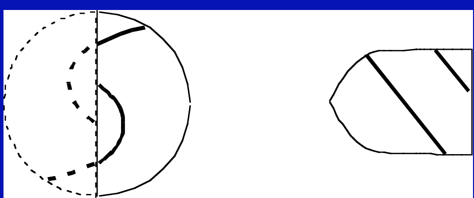
  $$\mathrm{Log}[(w(z)+a)/(w(z)+b)]$$

  where $w(z)$ wedges the argument.

- Left (G) : V1-V2-V3 (Horton & Hoyt 1991).
- Right (H) : fit with a wedge-dipole model (Schwartz 2002).



- Lines in V1 correspond qualitatively to spiral on the retina.

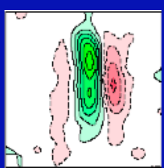


- In the linear approximation, (simple) neurons of V1 operate as filters on the optic signal coming from the retina.
- Their receptive fields (the bundle of photoreceptors they are connected with via the retino-geniculo-cortical pathways) have receptive profiles (transfert function) with a characteristic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

- 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.

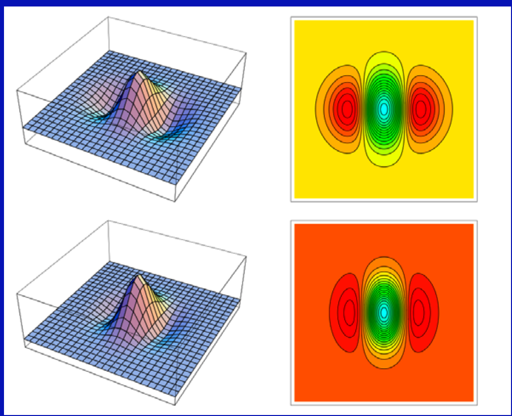
- For simple cells, RFs are highly anisotropic and elongated along a preferential orientation.
- Level curves of the receptive profiles can be recorded :



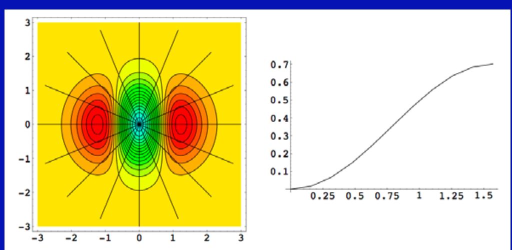
- The receptive profiles can be modeled either
  - by second order derivatives of Gaussians,
  - or by Gabor wavelets

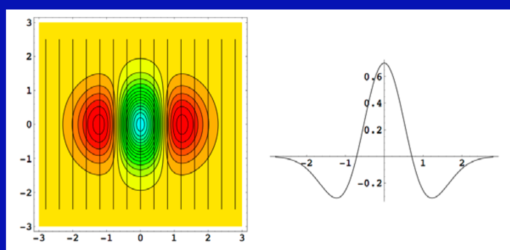
$$\exp(i2x)\exp\left(-\left(x^2+y^2\right)\right)$$

(real part).

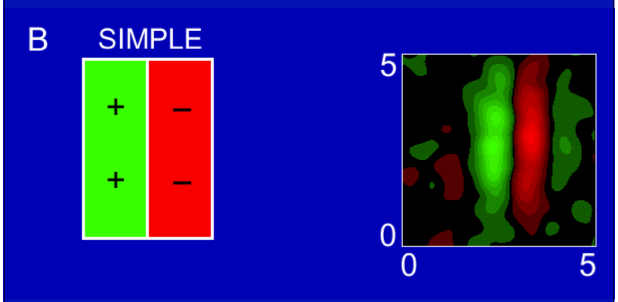


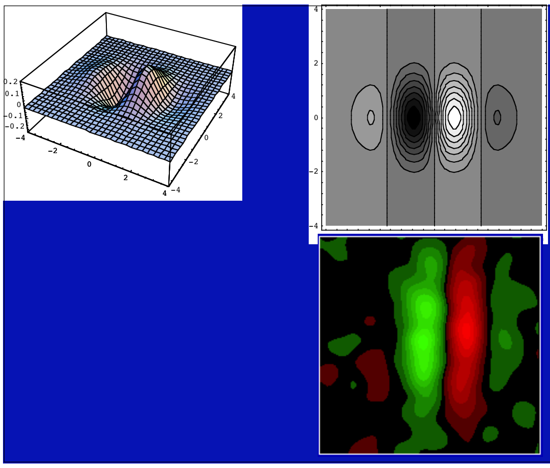
- There is a lot of technical discussions concerning the exact form of RP.
- Richard Young. « The Gaussian Derivative model for spatio-temporal vision », *Spatial Vision*, 14, 3-4, 2001, 261-319.
  - « The initial stage of processing of receptive fields in the visual cortex approximates a ‘derivative analyzer’ that is capable of estimating the local spatial and temporal directional derivatives of the intensity profile in the visual environment. »
- How ?



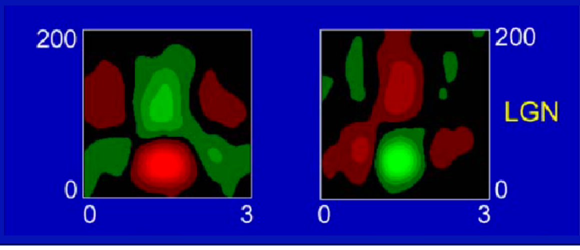


- There exist also RP of simple cells which are like third order derivatives of Gaussians (De Angelis).

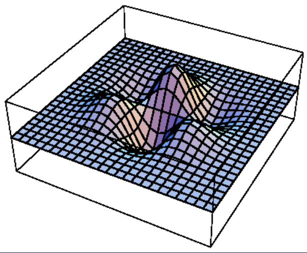


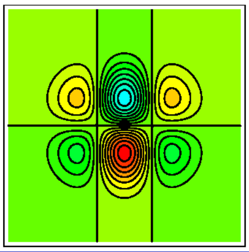


- If we add time (spatio-temporal RPs) we find third (and fourth) order derivatives.
  - White noise method. Correlation between (i) random sequences of flashed bright / dark bars at different positions, and (ii) sequences of spikes. The time is the correlation delay.



$$\frac{\partial^3 G}{\partial x^2 \partial t}$$

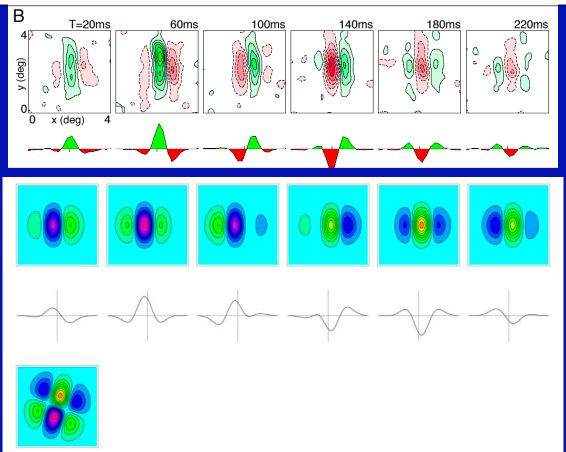




- Example of non separable spatio-temporal RPs: the ON/OFF regions evolve and this induces a selectivity to movement (velocity detection).

$$\frac{\partial^3 G}{\partial u^2 \partial v}$$

with plane (x, t) = plane (u, v) rotated of Pi/10.

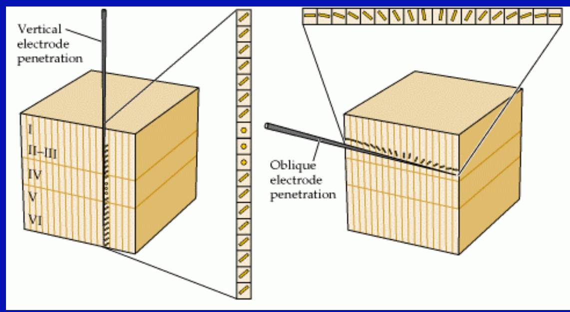


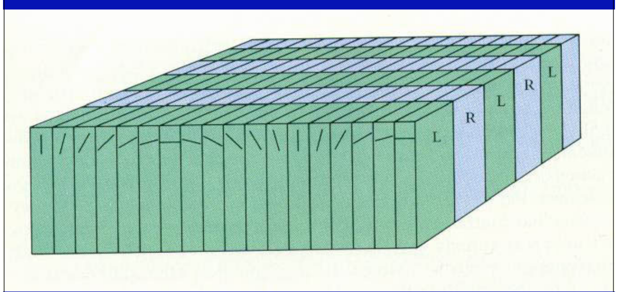
Hypercolumns and pinwheels

- 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.

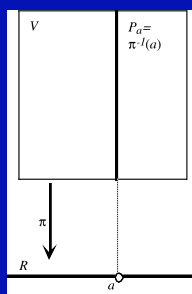
- For a given position $a = (x_0, y_0)$ in R, the simple neurons with variable orientations θ constitute an anatomically definable micromodule called an “hypercolumn”.
- The hypercolumns associate retinotopically to each position a of the retina R a full exemplar P_a of the space P of orientations p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

The functional architecture of area V1





- This functional architecture implements what is called in differential geometry the fibration $\pi : R \times P \to R$ with base R, fiber P, and total space $V = R \times P$.



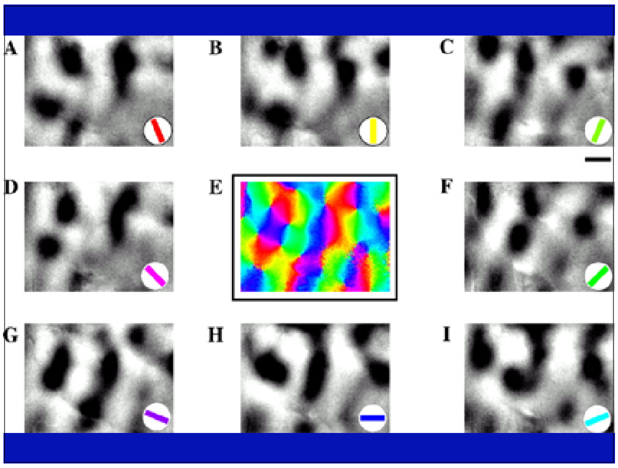
- Fibration formalizes Hubel 's concept of "engrafting" "secundary" variables (orientation, ocular dominance, color, direction of movement, etc.) on the basic retinal variables (x,y) :
  - « What the cortex does is map not just two but many variables on its two-dimensional surface. It does so by selecting as the basic parameters the two variables that specify the visual field coordinates (…), and on this map it engrafts other variables, such as orientation and eye preference, by finer subdivisions. » (Hubel 1988, p. 131)

Pinwheels

- The fibration $\pi : R \times P \to R$ is of dimension 3 but is implemented in neural layers W of dimension 2.

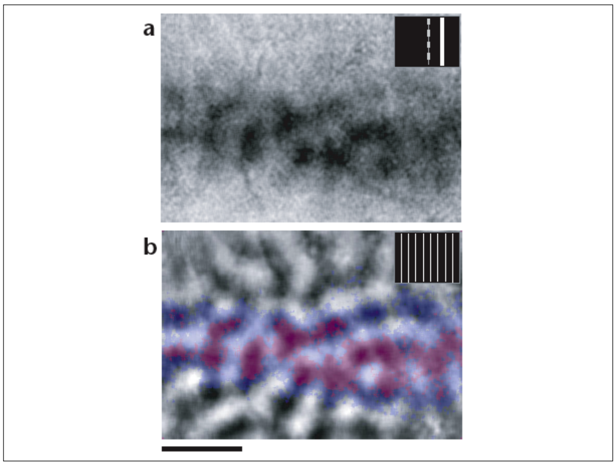
- Hypercolumns are geometrically organized in 2D-pinwheels.
- The cortical layer is reticulated by a network of singular points which are the centers of the pinwheels.
- Locally, around these singular points all the orientations are represented by the rays of a "wheel" and the local wheels are glued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

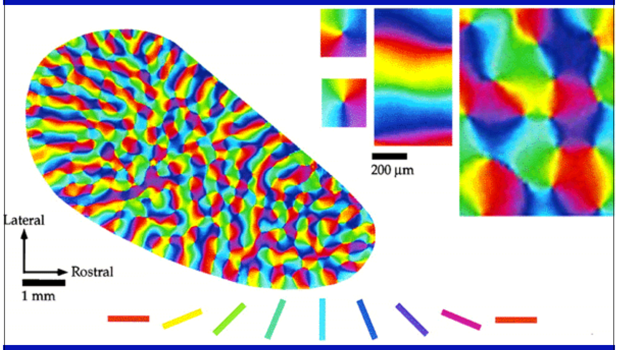


- At a certain resolution and with a population coding, a "point" corresponds to a small assembly of neurons with approximatively the same receptive field and the same preferred orientation.
- It codes a contact element (a, p).

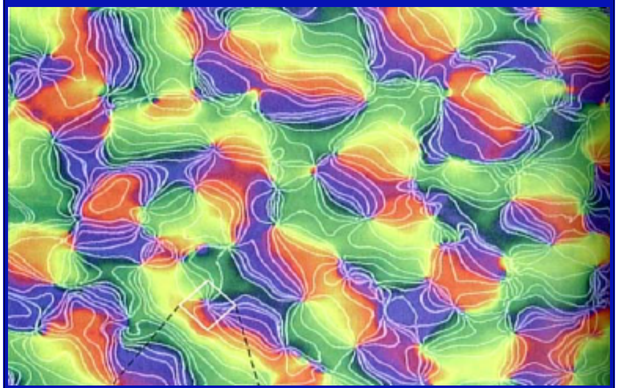
- The following picture shows
- (a) the sub-population (stripe) of V1 neurons activated by a <u>long</u> line stimulus located at a precise (vertical) position (scale bar = 1mm).
- (b) the embedding of the stripe in the population of V1 neurons responding to the same vertical orientation but at different positions.



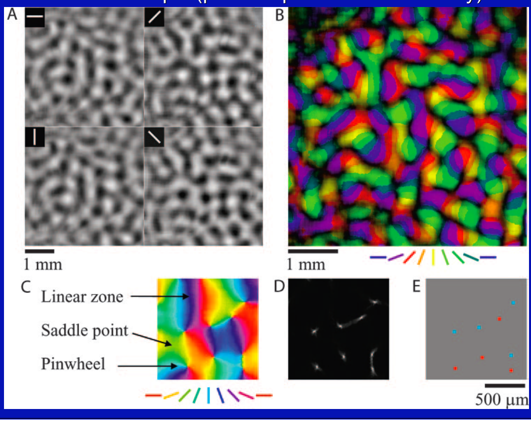
- In the following picture the orientations are coded by colors and iso-orientation lines are therefore coded by monocolor lines.
- William Bosking, Ying Zhang, Brett Schofield, David Fitzpatrick (Dpt of Neurobiology, Duke) 1997, « Orientation Selectivity and the Arrangement of Horizontal Connections in Tree Shrew Striate Cortex », *J. of Neuroscience*, 17, 6, 2112-2127.



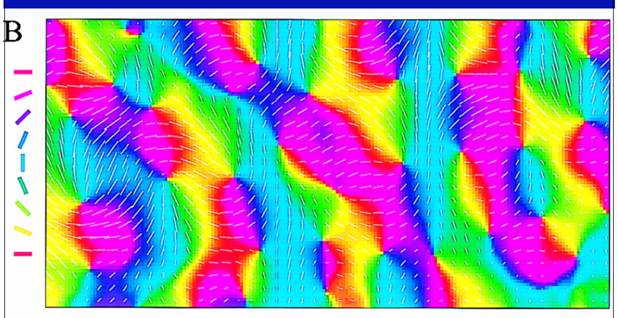
- There are 3 classes of points :
  - regular points where the orientation field is locally trivial;
  - singular points at the center of the pinwheels;
  - saddle-points localized near the centers of the cells of the network.
- Two adjacent singular points are of opposed chirality (CW and CCW).
- It is like a field in *W* generated by topological charges with « field lines » connecting charges of opposite sign.

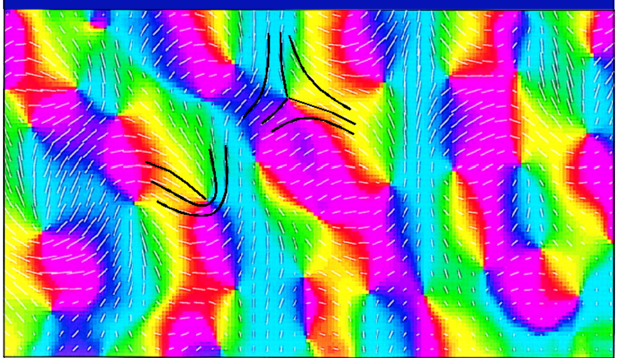


- Another example (primate: prosimian Bush Baby)



- In the following picture due to Shmuel (cat's area 17), the orientations are coded by colors but are also represented by white segments.
- We observe very well the two types of generic singularities of 1D foliations in the plane.





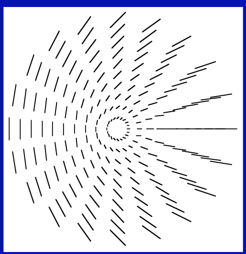
- They arise from the fact that, in general, the direction θ in V1 of a ray of a pinwheel is not the orientation p_θ associated to it in the visual field.
- When the ray spins around the singular point with an angle φ, the associated orientation rotates with an angle $\varphi/2$. Two diametrally opposed rays correspond to orthogonal orientations.
- There are two cases.

- If the orientation p_θ associated with the ray of angle θ is $p_\theta = \alpha + \theta/2$ (with $p_0 = \alpha$), the two orientations will be the same for

$$p_\theta = \alpha + \theta/2 = \theta$$

that is for $\theta = 2\alpha$.

- As α is defined modulo π, there is only one solution : end point.

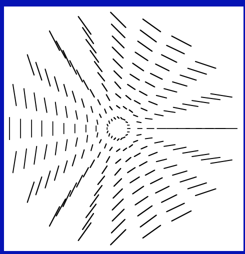


- If the orientation p_θ associated with the ray of angle θ is $p_\theta = \alpha - \theta/2$, the two orientations will be the same for

$$p_\theta = \alpha - \theta/2 = \theta$$

that is for $\theta = 2\alpha/3$.

- As α is defined modulo π, there are three solutions : triple point.



Wolf-Geisel model

- Fred Wolf and Theo Geisel modeled the pinwheel network using a complex field

$$Z : \mathbb{C} \to \mathbb{C},\ z = \rho e^{i\theta} \mapsto r(z)\, e^{i\varphi(z)}$$

where the spatial phase $\varphi(z)$ codes the orientation and the module $r(z)$ codes the orientation selectivity.

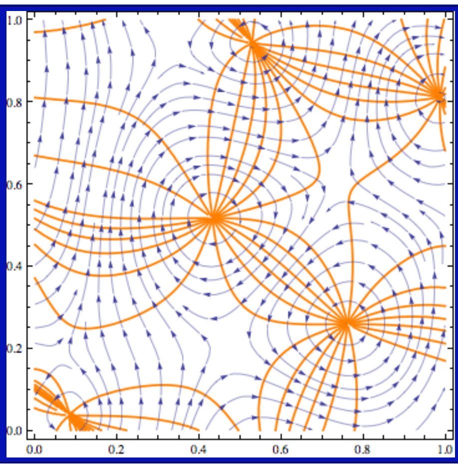
- Under the (non trivial) hypothesis that there is no selectivity at the pinwheel singularities, these are *zeroes* of the field.

- If $Z = X + iY$, pinwheels are the intersections of the curves $X = 0$ and $Y = 0$.
- They are analogous to *dislocations* in optical phase fields.
- There are two classes of curves:
  - the integral curves of the phase field,
  - the *isophase* curves called *wavefronts* in optics.

- The field orthogonal to the isophase curves is the gradient field of φ. But φ is undeterminate at the singularities.
- In such cases physicists use the *current* field

$$\mathcal{J} = r^2 \nabla \varphi.$$

$$\mathcal{J} = X\nabla Y - Y\nabla X$$

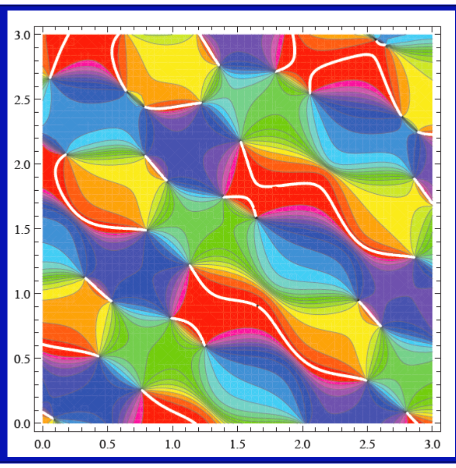


- To get phase fields with a characteristic length, it is convenient to use superpositions of *plane waves* sharing the same wave number *k* :

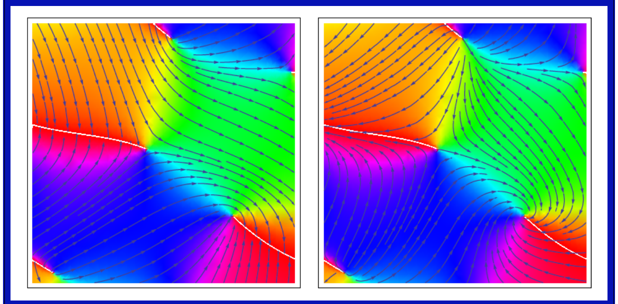
$$
\begin{aligned}
&Ae^{i\kappa . a}\\
&A = Ee^{i\phi} \text{ complex amplitude}\\
&\kappa = (\kappa_x, \kappa_y) \text{ wave vector}\\
&k = |\kappa| \text{ wave number}\\
&\Lambda = \frac{2\pi}{k} \text{ wave length}
\end{aligned}
$$

- They are solutions of the Helmholtz equation :

$$\Delta Z + k^2 Z = 0$$



- When we look at possible underlying orientation integral lines, we get again end points and triple points.



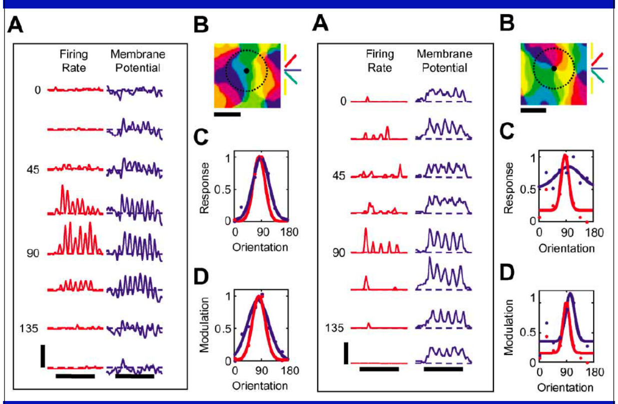
Micro-structure near pinwheel centers

- P. E. Maldonado, I. Gödecke, C. M. Gray, T. Bonhöffer (« Orientation Selectivity in Pinwheel Centers in Cat Striate Cortex », *Science*, 276 (1997) 1551-1555) have analyzed the fine-grained structure of orientation maps at the singularities. They found that

  « orientation columns contain sharply tuned neurons of different orientation preference lying in close proximity ».

- James Schummers « Synaptic integration by V1 neurons depends on location within the orientation map » (*Neuron*, 36, 2002, 969-978) has shown that
  - « neurons near pinwheel centers have subthreshold responses to all stimulus orientations but spike responses to only a narrow range of orientations ».
- Scales.
  - Left (far for from a pinwheel): 8 spikes/s, 10mV, 2s.
  - Right (at a pinwheel): 3 spikes/s, 8mV, 2s.

- Far from a pinwheel, cells « show a strong membrane depolarization response only for a limited range of stimulus orientation, and this selectivity is reflected in their spike responses ».
- At a pinwheel center, on the contrary, only the spike response is selective. There is a strong depolarization of the membrane for all orientations.
- The stimuli are moving oriented gratings.



- It is an original solution to the problem of singularities.
- But the spatial (50μ) and depth resolutions of optical imaging is not sufficient.
- One needs single neuron resolution to understand the micro-structure.

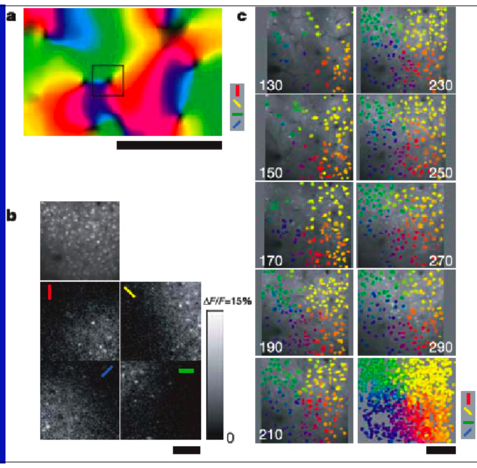
- What is the structure near singularities ?
- The spatial (50μ) and depth resolutions of optical imaging is not sufficient.
- One needs single neuron resolution to understand the micro-structure.

- 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) .

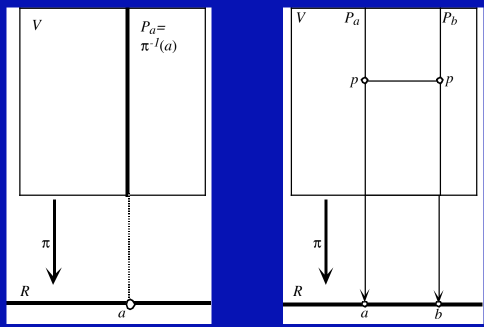
- (In cat) pinwheels are higly ordered at the micro level and « thus pinwheels centres truly represent singularities in the cortical map ».
- Injection of calcium indicator dye (Oregon Green BAPTA-1 acetoxylmethyl esther) which labels few thousands of neurons in a 300-600µ region.
- Two-photon calcium 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 <u>same</u> orientation wheel.
- « This demonstrates the columnar structure of the orientation map at a very fine spatial scale ».



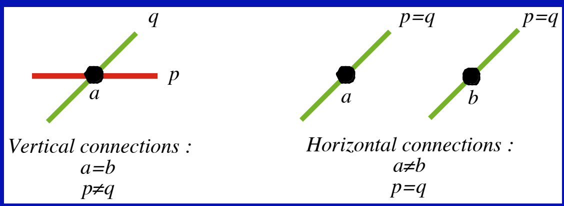
The horizontal structure

- 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.

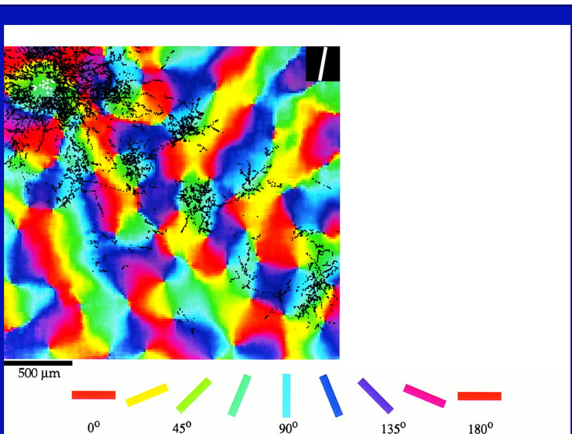


- Cortico-cortical connections are slow (≈ 0.2m/s) and weak.
- They connect neurons of almost similar orientation in neighboring hypercolumns.
- This means that the system is able to know, for b near a, if the orientation q at b is the same as the orientation p at a.

- The retino-geniculo-cortical "vertical" connections give an *internal* meaning for the relations between (*a*,*p*) and (*a*,*q*) (*different* orientations *p* and *q* at the *same* point *a*) .
- The "horizontal" cortico-cortical connections give an *internal* meaning for the relations between (*a*,*p*) and (*b*,*p*) (*same* orientation *p* at *different* points *a* and *b*).



- 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.

New models for pinwheels

- All orientations must be present with a good selectivity at the singularities but the selectivity can be subliminar or not .
- How can we model the dimensional collapse of the 3D abstract space

$$V = \mathbb{R}^2 \times \mathbb{P}^1$$

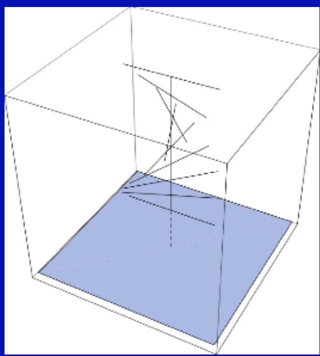
onto 2D neural layers ?

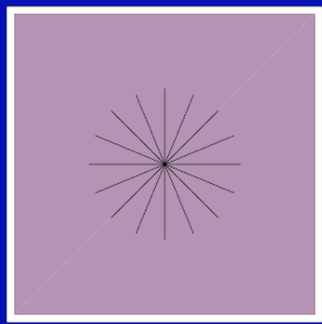
- An idea could be to use the concept of blowing-up.
- It is in some sense an intermediary dimension between 2D and 3D.
- It is an unfolding of a 2D orientation wheel along a third dimension.

- In an infinitesimal neighborhood of the blown up point, it is in the kernel of the differential 1-form

$$p = \frac{dy}{dx}$$

$$\omega = dy - pdx$$





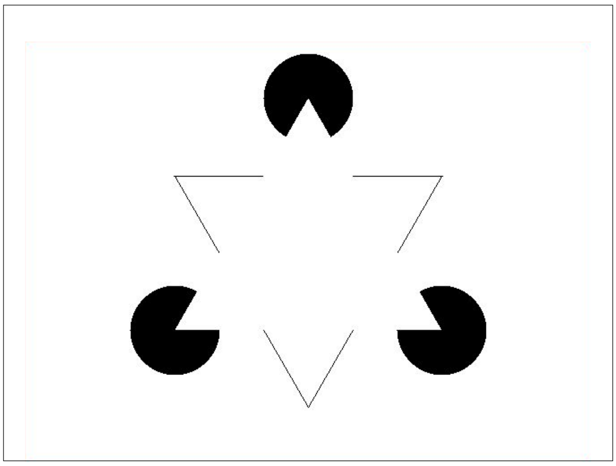
- One can blow-up in parallel several points a_i and glue the local pinwheels using a field endowing the a_i with topological charges (chirality).
- One gets that way a model of a network of pinwheels.

- Then, one can consider networks of points a_i with a mesh $\to 0$.
- One recovers

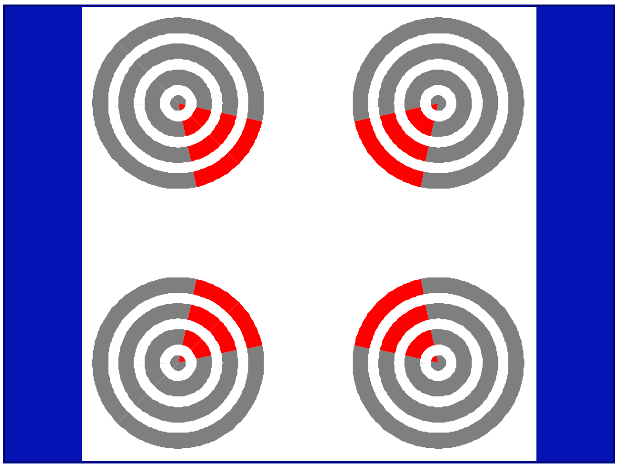
$$V = \mathbb{R}^2 \times \mathbb{P}^1$$

A typical example : Kanizsa illusory contours

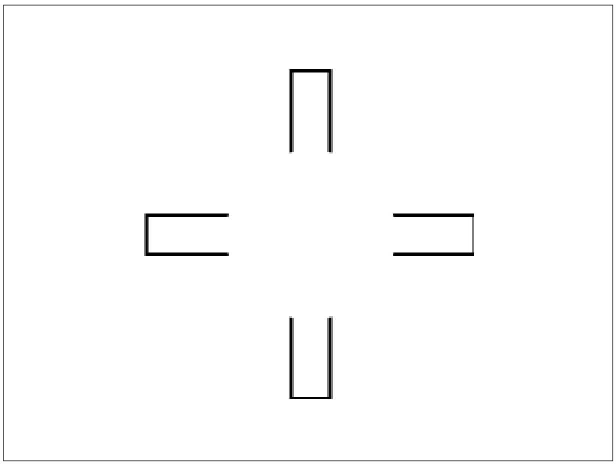
- A typical example of the problems of neurogeometry is given by well known Gestalt phenomena such as Kanizsa illusory contours.
- The visual system (V1 with some feedback from V2) constructs very long range and crisp virtual contours.



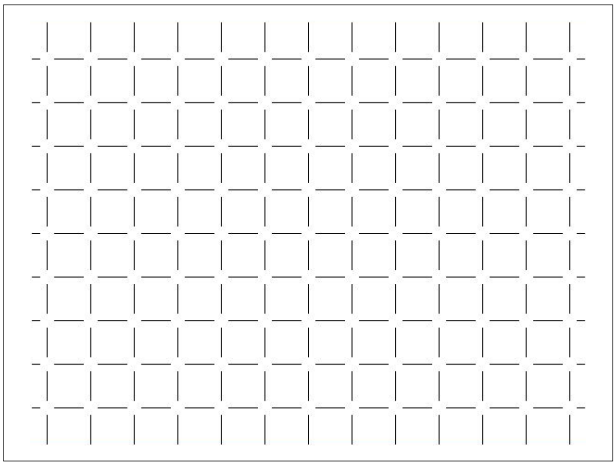
- They can even be *curved*.
- With the neon effect (watercolor illusion), virtual contours are boundaries for the diffusion of color inside them.



- 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 contact structure of V1

- The first model : the space of 1-jets of curves C in R.
- It is the beginning of what I call neurogeometry .

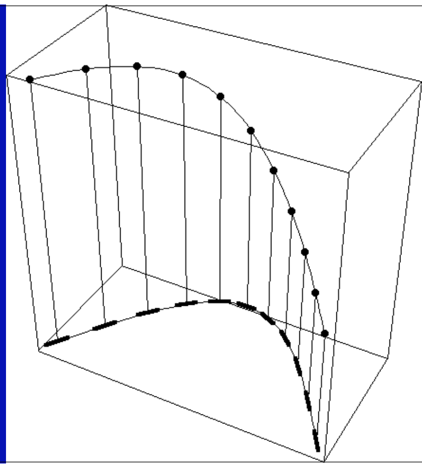
- If C is curve in R (a contour), it can be lifted to V. The lifting Γ is the map (1-jet)

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

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.

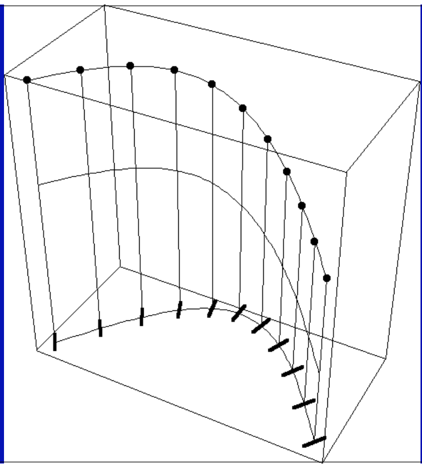


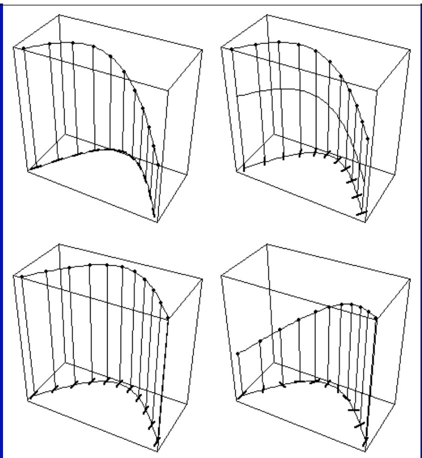
Fonctionality of jet spaces

- 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 an 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.





- Geometrically, the integrability condition means the following. Let (we suppose x is the basic variable)

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

be a *tangent vector* to V at the point

$$(a, p) = (x, y, p).$$

If $y' = p$ we have

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

- The integrability condition means that t is in the kernel of the 1-form

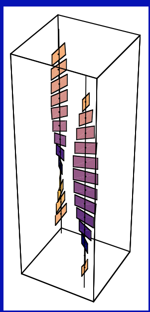
$$\omega = dy - p dx$$

$\omega = 0$ means simply $p = dy / dx$.

- But this kernel is in fact a plane called the contact plane of V at (a, p).

- The integrable curves are everywhere tangent to the field of contact planes.
- The vertical component p' of the tangent vector is then the *curvature* :

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



Contact structure and Heisenberg group

- The contact structure on V is left-invariant for a group structure which is isomorphic to the (polarized) Heisenberg group :

$$(x, y, p).(x', y', p') = (x + x', y + y' + px', p + p')$$

- If $t = (\xi, \eta, \pi)$ are the tangent vectors of $\mathfrak{V} = T_0 V$, the Lie algebra of V has the Lie bracket

$$[t, t'] = [(\xi, \eta, \pi), (\xi', \eta', \pi')] = (0, \xi'\pi - \xi\pi', 0)$$

- Lie algebra $X_1 = \partial_x + p\partial_y = (1, p, 0)$, and $X_2 = \partial_p = (0, 0, 1)$, we have :

$$[X_1, X_2] = X_3 = -\partial_y = (0, -1, 0)$$

  (other brackets = 0).

- It is essential to understand this geometry since it drives diffusion (heat equation) and propagation (wave equation) in V1.

- This Lie algebra can be represented by nilpotent matrices $m(\xi, \eta, \pi)$

$$\begin{pmatrix} 0 & \pi & \eta \\ 0 & 0 & \xi \\ 0 & 0 & 0 \end{pmatrix}$$

  and the elements (x, y, p) of the group V by matrices $M(x, y, p) = I + m(x, y, p)$

$$\begin{pmatrix} 1 & p & y \\ 0 & 1 & x \\ 0 & 0 & 1 \end{pmatrix}$$

Sub-Riemannian geometry

- In this neuro-geometrical framework, we can easily interpret the variational process giving rise to illusory contours.
- The key idea is to use a geodesic model in the sub-Riemannian geometry associated to the contact structure.
- This deepens the “elastica” model proposed by David Mumford.

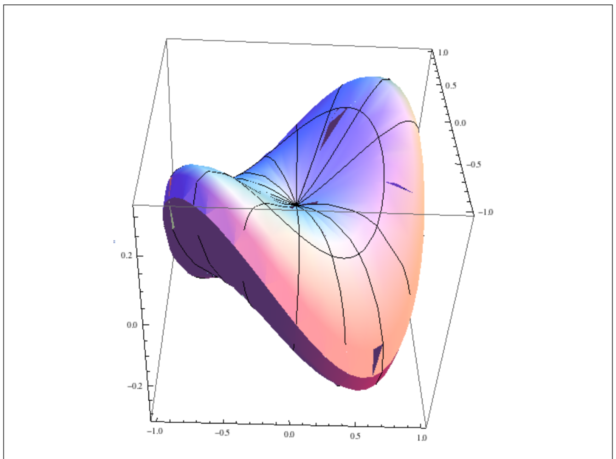
- If $\mathcal{K}$ is the contact structure on V and if one considers only curves Γ in V which are integral curves of $\mathcal{K}$, then metrics $g_{\mathcal{K}}$ defined only on the planes of $\mathcal{K}$ are called sub-Riemannian metrics.

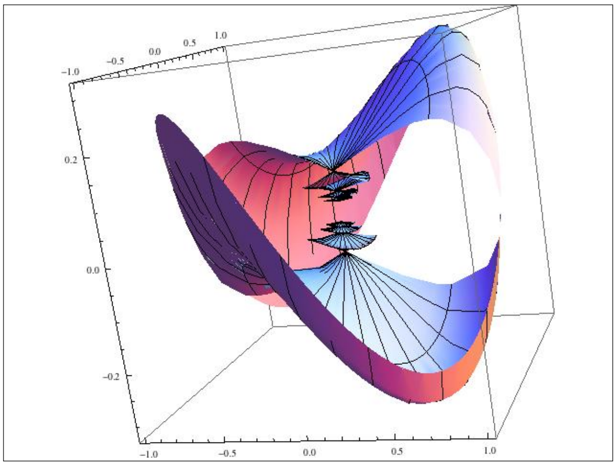
- In a Kanizsa figure, two pacmen of respective centers a and b with a specific aperture angle define two elements (a, p) and (b, q) of V.
- An illusory contour interpolating between (a, p) and (b, q) is
  - 1. a curve C from a to b in R with tangent p at a and tangent q at b;
  - 2. a curve minimizing an “energy” (variational problem), that is a geodesic for some sub-Riemannian metric.

- For a model isomorphic to the space of 1-jets (the Heisenberg group), Richard Beals, Bernard Gaveau and Peter Greiner have solved the problem.
- They claimed :
  - “The results indicate how complicated a control problem can become, even in the simplest situation.”

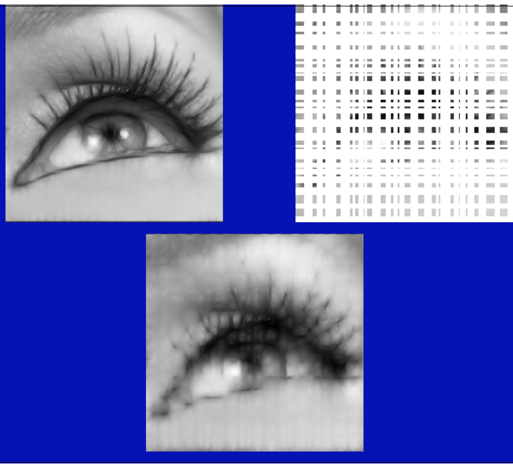
- In 1977 Bernard Gaveau still said:
  - "Le problème variationnel est le problème de minimiser l'énergie d'une courbe de la variété de base sous la condition de Lagrange que son relèvement horizontal est fixé dans le fibré. Ce problème semble non étudié.'"

- It is natural to take on the contact planes the metric making orthonormal their evident generators : $X_1 = \partial_x + p\partial_y$, $X_2 = \partial_p$ whose Lie bracket is $[X_1, X_2] = -X_3 = -\partial_y$.
- The structure of geodesics implies that the sub-Riemannian sphere S and the wave front W (geodesics of SR length 1) are rather strange. We can compute them explicitely (it is a variant of Beals *et al.* computations).





- Using sub-Riemannian (highly anisotropic) diffusion along sub-Riemannian geodesics, one can do inpainting.
- The results are rather spectacular.



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