Rapport du CREA, Ecole Polytechnique, 2014

Wilson-Cowan equations, functional architecture of $V1$ and bifurcations of visual patterns under symmetry-breaking

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1 Introduction

Paul Bressloff, Jack Cowan, and Martin Golubitsky proposed a deep explanation of geometric visual hallucinations.

Previous works of Bard Ermentrout and Jack Cowan

The spontaneously emerging and geometrically well behaved visual patterns are modeled as

1. eigenforms
2. deriving from a spontaneous symmetry-breaking
3. of a steady-state homogeneous solution
4. of the PDE which drives the activity of the striate cortex $V1$.

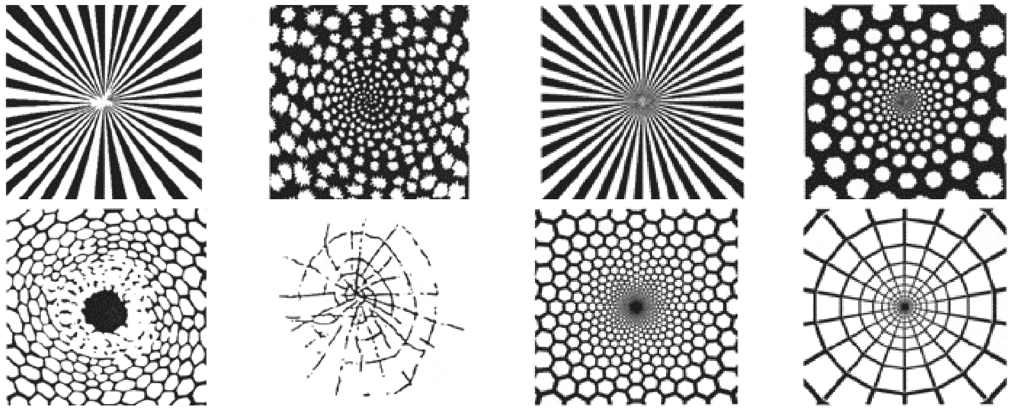
Key idea:

1. the symmetry group $E(2)$ of the retinal plane $R = \mathbb{R}^2$ acts on the *functional architecture* FA of $V1$,
2. this functional architecture FA is itself encoded in the synaptic weights of the PDE.

The constraints imposed by this group equivariance are extremely strong:

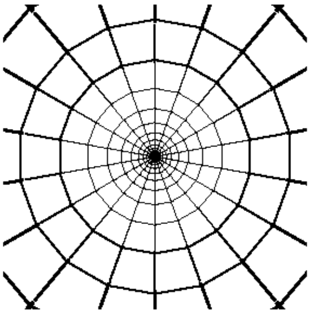
the geometry of the bifurcating patterns can be quite enterely deduced from it.

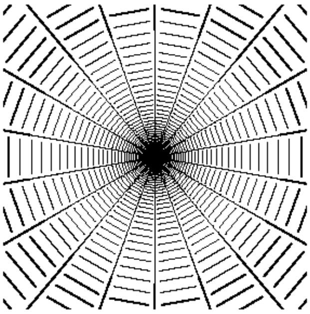
The fit of the models with empirical data is astonishing (Table 1).

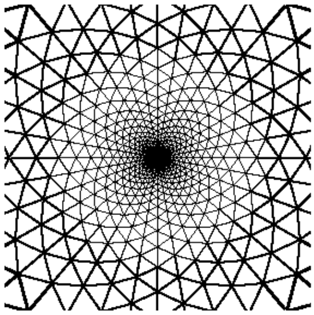


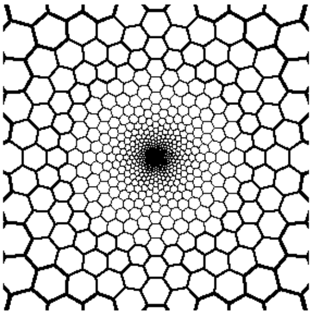
1. Drawings of visual hallucinations. 2. Their mathematical models.

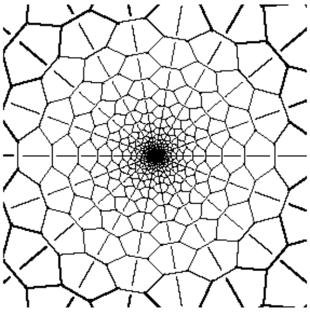
Table 1


1. Even squares.


2. Even rolls.


3. Even hexagons I.


4. Even hexagons II.


5. Even rhombs.

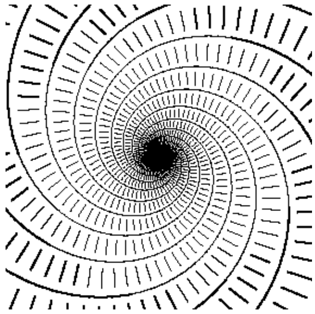
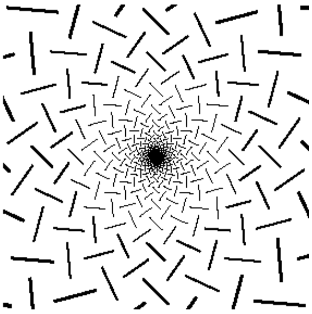
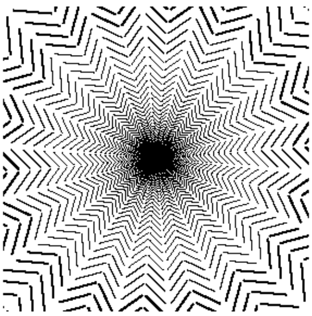
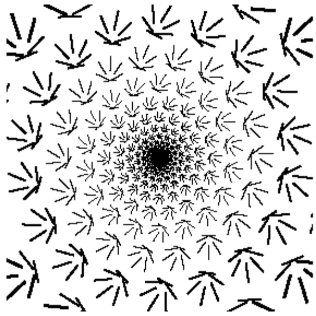
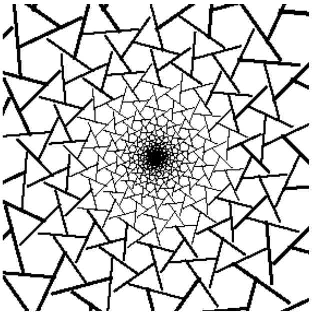

6. Even rhombic rolls.

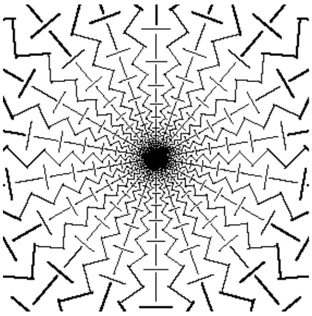
Table 13


1. Odd squares.


2. Odd rolls.


3. Odd hexagons I (triangles).


4. Odd hexagons II.


5. Odd rhombs.

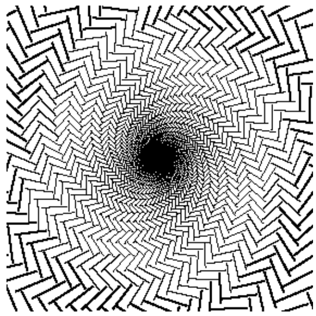
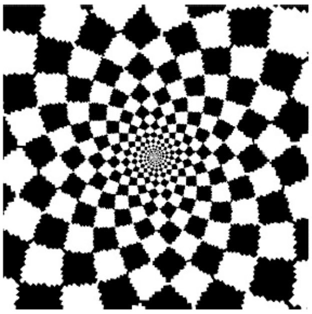
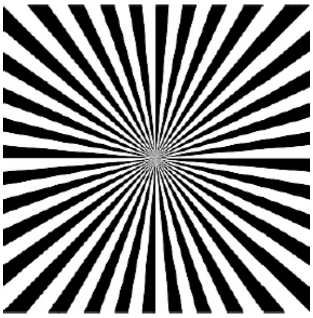

6. Odd rhombic rolls.

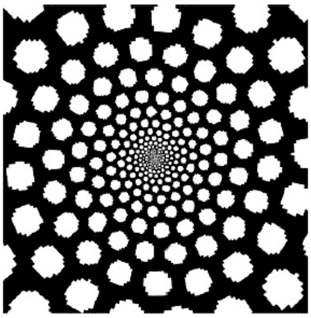
Table 14



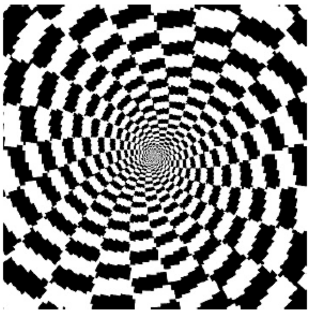
1. Non-contoured squares.



2. Non-contoured rolls.



3. Non-contoured hexagons.



4. Non-contoured rhombs.

Table 15

Papers used in the presentation:

1. Bard Ermentrout, Jack Cowan : " A mathematical theory of visual hallucinations ", *Biol. Cybernetics*, 34 (1979) 137-150.

2. Paul Bressloff, Jack Cowan, Martin Golubitsky, Peter Thomas, and Matthew Wiener: " Geometric visual hallucinations, Euclidean symmetry and the functional architecture of striate cortex ", *Phil. Trans. R. Soc. Lond. B* 356 (2001) 299-330.

3. Bressloff, Cowan, Golubitsky, Thomas: " Scalar and pseudoscalar bifurcations with application to pattern formation on the visual cortex " (to appear).

4. Bressloff, Cowan: " The functional geometry of local and horizontal connections in a model of V1 ", *Neurogeometry and Visual Perception* (J. Petitot, J. Lorenceau, eds.), *J. Physiology (Paris)*, 97, 2-3 (2003) 221-236.

Acknowledgement: Yves Frégnac.

2 Some empirical data

2.1 Klüver's first data

Geometrical patterns perceived after exposure to a violent flickering light, absorption of substances such as mescaline, LSD, psilocybin, ketamin, some alkaloids (peyote), or after near death experiences.

It is known that subjects see spontaneously and vividely typical forms such as tunnels and funnels, spirals, lattices (honeycombs, triangles), cobwebs, etc.

> " Such visual imagery is dynamic and the illusory contours usually explode from the center of gaze to the periphery, appearing initially in black and white before bright colors take over, and eventually pulsate and rotate in time as the experience progresses " (Frégnac).

These illusory forms were already classified in 1928 by Heinrich Klüver (1897-1979).

> " Klüver's interest in mescal 'buttons' or peyote (...) can be traced back to his earlier publications on eidetic visual phenomena, for mescal visions were thought to resemble visual eidetic imagery. (...) He experienced recurring visual forms (...). Klüver always recognized the importance of his data for other fields, and he confidently pointed out that psychoactive compounds were an important tool in the study of visual abilities such as color and space phenomena, dreams, illusions, and hallucinations. "

2.2 The NIMH programs

Programs at the National Institute of Mental Health aiming at probing neuroreceptors with varied substances in order to investigate the chemical architecture of the mind.

One locates each substance in an abstract “receptor space” with one axis for each receptor.

Thomas Ray (Univ. of Oklahoma):

> Substances “ shift the balance of activity of the brain away from the origin, by a vector representing the profile of binding affinities at different receptors. ”

3 The functional architecture of V1

The retino-geniculo-cortical vertical connections provide an internal meaning for the relations $(\mathbf{x}, p) - (\mathbf{x}, q)$ (different orientations p and q at the same point $\mathbf{x}$)

The horizontal cortico-cortical connections provide an internal meaning for the relations $(\mathbf{x}, p) - (\mathbf{y}, p)$ (same orientation p at different points $\mathbf{x}$ and $\mathbf{y}$).

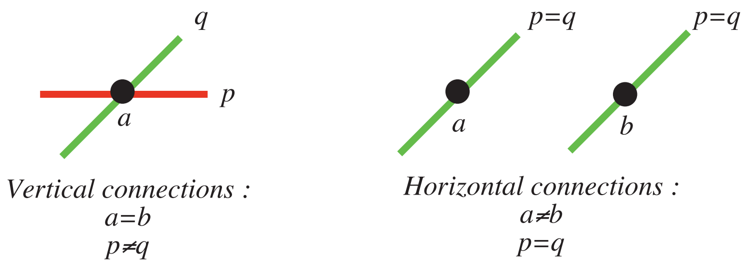


Figure 1: The two local structures of the functional architecture of $V1$.

Moreover, horizontal connections connect neurons not only parallel (co-oriented), but also *co-axial*: $p =$ orientation of $\mathbf{xy}$.

Bosking:

> " The system of long-range horizontal connections can be summarized as preferentially linking neurons with co-oriented, co-axially aligned receptive fields ".

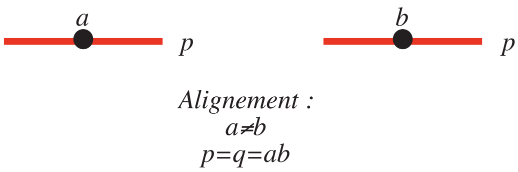


Figure 2: Alignement and coaxiality of two simple cells of $V1$.

3.1 The E(2)-invariance of the functional architecture

The FA of $V1$ is *invariant* under the action of the Euclidean group $E(2) = O(2) \dot{+} \mathbb{R}^2$ of isometries (rigid motions and reflexions) of the affine plane.

$E(2)$ is the semi-direct product $\dot{+}$ of the orthogonal group $O(2)$ (rotation group $SO(2)$ plus reflexions) with the translation group $\mathbb{R}^2$.

Let $(\mathbf{y}, r_\theta) \in E(2)$, $(\mathbf{y}, r_\theta)$ acts on $\mathbf{x} \in R$ by

$$(\mathbf{y}, r_\theta)(\mathbf{x}) = \mathbf{y} + r_\theta(\mathbf{x}) \ . \tag{1}$$

Non commutative product:

$$(\mathbf{z}, r_\varphi) \circ (\mathbf{y}, r_\theta) = (\mathbf{z} + r_\varphi(\mathbf{y}), r_{\varphi+\theta}) \ . \tag{2}$$

$$(\mathbf{y}, r_\theta) \circ (\mathbf{z}, r_\varphi) = (\mathbf{y} + r_\theta(\mathbf{z}), r_{\theta+\varphi}) \tag{3}$$

Of course $r_{\varphi+\theta} = r_{\theta+\varphi}$, but $\mathbf{z} + r_\varphi(\mathbf{y}) \neq \mathbf{y} + r_\theta(\mathbf{z})$.

The rotation r_θ acts on the fibration $\pi : R \times P \to P$ by

$$r_\theta(\mathbf{x}, \varphi) = (r_\theta(\mathbf{x}), \varphi + \theta) \tag{4}$$

This action warrants that the alignement of preferred directions is $E(2)$-invariant.

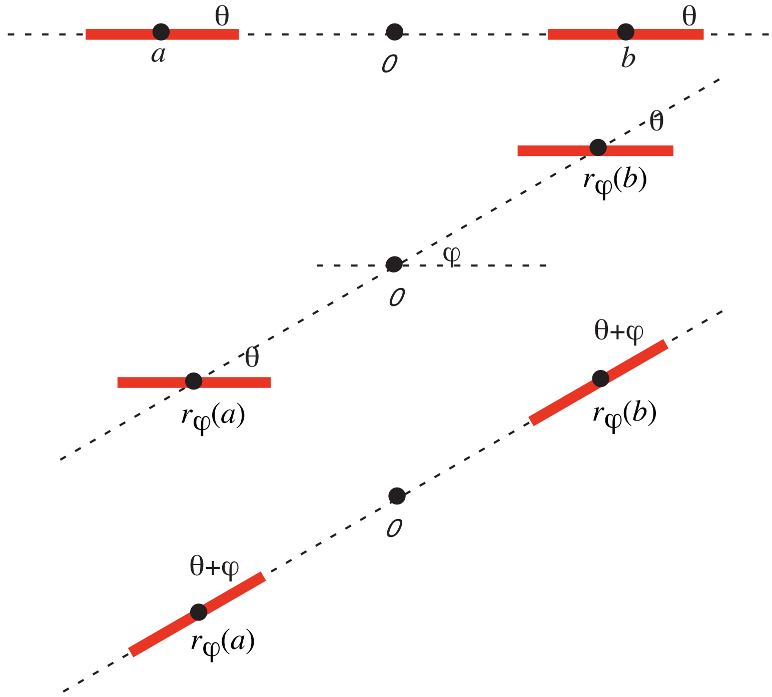


Figure 3: The $E(2)$ invariance of the functional architecture.

4 The Wilson-Cowan equations of V1

4.1 From Hopfield ODE to Wilson-Cowan PDE

The authors work in the fibration $\pi : V = R \times \mathbb{S}^1 \to R$ with local coordinates $(\mathbf{x}, \varphi)$.

Neurons $(\mathbf{x}, \varphi)$ have an activity $a(\mathbf{x}, \varphi, t)$ and are connected by connections with synaptic weights $w \langle \mathbf{x}, \varphi \mid \mathbf{x}', \varphi' \rangle$.

We look for the PDE governing $a(\mathbf{x}, \varphi, t)$.

Hopfield equations. Let $u_i, i = 1, ..., N$ be formal neurons with activity $a_i(t)$.

If time and space are discrete:

$$a_i(t+1) = \sum_{j=1}^{j=N} w_{ij} \sigma\left(a_j(t)\right) + h_i(t)$$

$\sigma =$ non linear gain function (with $\sigma(0) = 0$),
$w_{ij} =$ weight of the connection between u_i and u_j,
$h =$ external input.

If time is continuous and space discrete, system of N ordinary differential equations (ODE):

$$\frac{da_i}{dt}(t) = -a_i(t) + \sum_{j=1}^{j=N} w_{ij}\sigma\left(a_j(t)\right) + h_i(t)$$

If time and space are continuous, partial differential equation (PDE):

$$\frac{\partial a(v,t)}{\partial t} = -a(v,t) + \int_V w\left\langle v|v'\right\rangle \sigma\left(a(v',t)\right) dv' + h(v,t)$$

(where $v \in V$ is a point in the configuration space).

The authors use the following PDE:

$$\frac{\partial a(\mathbf{x},\varphi,t)}{\partial t} = -\alpha a(\mathbf{x},\varphi,t) \quad (5)$$
$$+\frac{\mu}{\pi}\int_0^{\pi}\int_R w\left\langle \mathbf{x},\varphi|\mathbf{x}',\varphi'\right\rangle \sigma\left(a(\ \mathbf{x}',\varphi',t)\right) d\mathbf{x}'d\varphi' + h(\mathbf{x},\varphi,t) \quad (6)$$

$w\left\langle \mathbf{x},\varphi|\mathbf{x}',\varphi'\right\rangle$ = weight of the connection between the neuron $v = (\mathbf{x},\varphi)$ and the neuron $v' = (\mathbf{x}',\varphi')$,

α = parameter of decay,

μ = parameter of excitability of $V1$.

μ is an example of localization of a substance in a receptor space.

4.2 The encoding of the functional architecture in the synaptic weights

Key point: *the functional architecture AF of $V1$ can be encoded in the weights* $w\left\langle \mathbf{x},\varphi|\mathbf{x}',\varphi'\right\rangle$.

1. Local vertical connections inside a single hypercolumn $\Longrightarrow$:

$$w\left\langle \mathbf{x},\varphi|\mathbf{x}',\varphi'\right\rangle = w_{loc}\left(\varphi-\varphi'\right)\delta\left(\mathbf{x}-\mathbf{x}'\right) \tag{7}$$

   $w_{loc}\left(\varphi\right)$ *even* function and $\delta\left(\mathbf{x}-\mathbf{x}'\right)$ (δ the Dirac function) forces $\mathbf{x}=\mathbf{x}'$.

2. Lateral horizontal connections between different hypercolumns $\Longrightarrow$:

$$w\left\langle \mathbf{x},\varphi|\mathbf{x}',\varphi'\right\rangle = w_{lat}\left(\mathbf{x}-\mathbf{x}',\varphi\right)\delta\left(\varphi-\varphi'\right) \tag{8}$$

   $\delta\left(\varphi-\varphi'\right)$ forces $\varphi=\varphi'$ (horizontal connections connect pairs $(\mathbf{x},\varphi)$ and $(\mathbf{y},\varphi)$ with same φ).

3. Coaxiality condition $p=q=\mathbf{xy}\Longrightarrow$

$$w_{lat}\left(\mathbf{x}-\mathbf{x}',\varphi\right) = w_{lat}\left(s\right)\delta\left(\mathbf{x}-\mathbf{x}'-se_{\varphi}\right) = \hat{w}\left(r_{-\varphi}\left(\mathbf{x}-\mathbf{x}'\right)\right) \tag{9}$$

   $e_{\varphi}=$ unit vector in the direction φ.

4. *Specific* expression for the synaptic weights:

$$w\left\langle \mathbf{x},\varphi|\mathbf{x}',\varphi'\right\rangle = w_{loc}\left(\varphi-\varphi'\right)\delta\left(\mathbf{x}-\mathbf{x}'\right)+\beta\hat{w}\left(r_{-\varphi}\left(\mathbf{x}-\mathbf{x}'\right)\right)\delta\left(\varphi-\varphi'\right) \tag{10}$$

   $\beta=$ coefficient measuring the relative strength of the vertical and horizontal connections.

5. The PDE is then (for an input $h(\mathbf{x},\varphi,t)=0$):

$$\frac{\partial a(\mathbf{x},\varphi,t)}{\partial t} = -\alpha a(\mathbf{x},\varphi,t)+ \tag{11}$$

$$\mu\left[\int_0^{\pi} w_{loc}\left(\varphi-\varphi'\right)\sigma\left(a(\mathbf{x},\varphi',t)\right)\frac{d\varphi'}{\pi}\right]+$$

$$\mu\left[\beta\int_R w_{lat}\left(\mathbf{x}-\mathbf{x}',\varphi\right)\sigma\left(a(\mathbf{x}',\varphi,t)\right)d\mathbf{x}'\right]. \tag{12}$$

4.3 The E(2)-equivariance of the PDE

Action of the Euclidean group $E(2) = O(2) \dotplus \mathbb{R}^2$on $V1 = \mathbb{R}^2 \times S^1$: the *shift-twist* action

$$\begin{cases} \mathbf{y}(\mathbf{x},\varphi) = (\mathbf{x}+\mathbf{y},\varphi) \\ \theta(\mathbf{x},\varphi) = (r_\theta \mathbf{x}, \varphi+\theta) \\ \kappa(\mathbf{x},\varphi) = (\kappa\mathbf{x}, -\varphi) \end{cases}$$

If $a(\mathbf{x},\varphi)$ is a function $a : R \times S^1 \to \mathbb{R}$ and $\gamma \in E(2)$, by definition $\gamma a(\mathbf{x},\varphi) = a\left(\gamma^{-1}(\mathbf{x},\varphi)\right)$.

For the synaptic weights, by definition

$$\gamma w \left\langle \mathbf{x},\varphi|\mathbf{x}',\varphi'\right\rangle = w\left\langle \gamma^{-1}(\mathbf{x},\varphi)|\gamma^{-1}(\mathbf{x}',\varphi')\right\rangle .$$

Due to their *specific form*, the synaptic weights are $E(2)$-*invariant*.

1. Invariance trivial for the translations $\mathbf{y} \in R$: w depends only on $\mathbf{x}-\mathbf{x}'$ and $(\mathbf{x}+\mathbf{y})-(\mathbf{x}'+\mathbf{y}) = \mathbf{x}-\mathbf{x}'$.

2. For the rotations γ^{-1} gives $r_{-\theta}\mathbf{x}$ and $\varphi-\theta$:

$$\begin{aligned} & w\left\langle r_{-\theta}\mathbf{x},\varphi-\theta|r_{-\theta}\mathbf{x}',\varphi'-\theta\right\rangle \\ =\, & w_{loc}\left((\varphi-\theta)-(\varphi'-\theta)\right)\delta\left(r_{-\theta}\mathbf{x}-r_{-\theta}\mathbf{x}'\right)+ \\ & \beta\hat{w}\left(r_{-(\varphi-\theta)}\left(r_{-\theta}\mathbf{x}-r_{-\theta}\mathbf{x}'\right)\right)\delta\left((\varphi-\theta)-(\varphi'-\theta)\right) \\ =\, & w_{loc}\left(\varphi-\varphi'\right)\delta\left(\mathbf{x}-\mathbf{x}'\right)+\beta\hat{w}\left(r_{-\varphi}\left(\mathbf{x}-\mathbf{x}'\right)\right)\delta\left(\varphi-\varphi'\right) \\ =\, & w\left\langle \mathbf{x},\varphi|\mathbf{x}',\varphi'\right\rangle \end{aligned}$$

3. For the reflexion κ:

$$\begin{aligned} & w\left\langle \kappa\mathbf{x},-\varphi|\kappa\mathbf{x}',-\varphi'\right\rangle \\ =\, & w_{loc}\left(-\varphi+\varphi'\right)\delta\left(\kappa\mathbf{x}-\kappa\mathbf{x}'\right)+\beta\hat{w}\left(r_{\varphi}\left(\kappa\mathbf{x}-\kappa\mathbf{x}'\right)\right)\delta\left(-\varphi+\varphi'\right) \\ =\, & w_{loc}\left(\varphi-\varphi'\right)\delta\left(\mathbf{x}-\mathbf{x}'\right)+\beta\hat{w}\left(r_{-\varphi}\left(\mathbf{x}-\mathbf{x}'\right)\right)\delta\left(\varphi-\varphi'\right) \\ =\, & w\left\langle \mathbf{x},\varphi|\mathbf{x}',\varphi'\right\rangle \end{aligned}$$

   since w_{loc} is even, $r_\varphi\kappa = \kappa r_{-\varphi}$ and $\hat{w}\left(\kappa\mathbf{x}\right) = \hat{w}\left(\mathbf{x}\right)$.

The $E(2)$-invariances imply that the PDE

$$\frac{\partial a(\mathbf{x},\varphi,t)}{\partial t} = F\left(a(\mathbf{x},\varphi,t)\right)$$

(we suppose the input $h = 0$, that is we look for spontaneous patterns) is $E(2)$-*equivariant*: $\gamma F(a) = F(\gamma a)$.

Martin Golubitsky,

> “ The equivariance of the operator F with respect to the action of $E(2)$ has major implications for the nature of solutions bifurcating from the homogeneous resting state. ”

5 Bifurcations and emerging patterns ($h = 0$)

How macro morphologies can spontaneously emerge in such a geometrically structured neural network?

For $\mu = 0$, $a \equiv 0$ is trivially the equilibrium state of the network and it is stable.

This initial state $a \equiv 0$ can become *unstable* and *bifurcate* for *critical* values μ_c of the parameter μ.

The increasing of μ models an increasing of the excitability of $V1$ due to the action of the substances on the nuclei (locus coeruleus, raphé) which produce neurotransmitters such as serotonin or noradrenalin.

The new stable states *present highly structured spatial patterns generated by a $E(2)$-symmetry breaking.*

The spectral analysis of the PDE and the analysis of bifurcations are rather technical:

1. –Linearization of the PDE near the solution $a \equiv 0$ and the critical value μ_c: $\sigma(a) \to \sigma'(0)a$
2. – Spectral analysis of the linearized equation. Computation of its eigenvectors (eigenmodes).
3. – We look at solutions of the form:

   $$a(\mathbf{x}, \varphi, t) = e^{\lambda t} a(\mathbf{x}, \varphi) \tag{13}$$

   where a temporal exponential $e^{\lambda t}$ modulates a spatial pattern $a(\mathbf{x}, \varphi)$. When $\mu = 0$, the solutions of the linear PDE

   $$\frac{\partial a(\mathbf{x}, \varphi, t)}{\partial t} = -\alpha a(\mathbf{x}, \varphi, t)$$

   are $a(\mathbf{x}, \varphi, t) = e^{-\alpha t} a(\mathbf{x}, \varphi)$.
4. – The solutions $a(\mathbf{x}, \varphi, t) = e^{\lambda t} a(\mathbf{x}, \varphi)$ are stationary only if $\lambda = 0$. Otherwise they decay ($\lambda < 0$, it is in particular the case for $\lambda = -\alpha$ which decays exponentially to 0) or diverge ($\lambda > 0$) exponentially.
5. - Substituting the solution in the linearized PDE, we get an equation for the eigenvalues λ of the form:

   $$\begin{aligned} &\lambda a(\mathbf{x}, \varphi) \\ &= -\alpha a(\mathbf{x}, \varphi) + \sigma'(0)\mu \left(\int_0^\pi w_{loc}(\varphi - \varphi') a(\mathbf{x}, \varphi') \frac{d\varphi'}{\pi} \right) \\ &+\sigma'(0)\mu \left(\beta \int_R w_{lat}(\mathbf{x} - \mathbf{x}', \varphi) a(\mathbf{x}', \varphi) d\mathbf{x}' \right). \end{aligned}$$

6. - Using Fourier series of a, w_{loc} and w_{lat} for the *periodic* variable φ and Fourier transforms for the spatial variable $\mathbf{x}$, and identifying the coefficients of the terms of the two sides of this equation we get *dispersion relations* of the form $\lambda = -\alpha + \mu F(...)$ where F is a function of the Fourier coefficients.
7. - For $\mu = 0$, $\lambda = -\alpha$. When μ increases, λ will vanish for the first time for a certain F and a certain critical value μ_c.
8. - The bifurcation will activate the corresponding Fourier modes.
9. - *Symmetries* imply extremely strong constraints.
10. - Finally we have to study the *stability* of the solutions.

6 Fourier expansions and dispersion relations

We linearize the PDE near the trivial solution $a \equiv 0$ and look for solutions of the form:

$$a(\mathbf{x}, \varphi, t) = e^{\lambda t} a(\mathbf{x}, \varphi) \tag{14}$$

We get

$$\begin{aligned}
&\lambda a(\mathbf{x}, \varphi) \qquad (15)\\
=&-\alpha a(\mathbf{x}, \varphi) + \sigma'(0)\mu \left(\int_0^{\pi} w_{loc}(\varphi - \varphi') a(\mathbf{x}, \varphi') \frac{d\varphi'}{\pi} \right)\\
&+\sigma'(0)\mu \left(\beta \int_R w_{lat}(\mathbf{x} - \mathbf{x}', \varphi) a(\mathbf{x}', \varphi) d\mathbf{x}' \right).
\end{aligned}$$

where the coefficient $\sigma'(0)$ comes from the linearization of the non linear gain function σ . We look at solutions where the spatial part is a *plane wave* of wave vector $\mathbf{k} = q(\cos\psi, \sin\psi)$ modulated by a *phase function* u (with the angle ψ of $\mathbf{k}$ as origin for the angular variable φ):

$$a(\mathbf{x}, \varphi) = u(\varphi - \psi) e^{i\mathbf{k}.\mathbf{x}} + c.c.$$

$a(\mathbf{x}, \varphi + \psi) = u(\varphi) e^{i\mathbf{k}.\mathbf{x}}$ and, substituting this form in equation (15 with φ substituted by $\varphi + \psi$) we get

$$\begin{aligned}
\lambda u(\varphi) e^{i\mathbf{k}.\mathbf{x}} =& -\alpha u(\varphi) e^{i\mathbf{k}.\mathbf{x}} +\\
&\sigma'(0)\mu \left(\int_0^{\pi} w_{loc}(\varphi + \psi - \varphi' - \psi) u(\varphi') e^{i\mathbf{k}.\mathbf{x}} \frac{d\varphi'}{\pi} \right) +\\
&\sigma'(0)\mu \left(\beta \int_R w_{lat}(\mathbf{x} - \mathbf{x}', \varphi + \psi) u(\varphi) e^{i\mathbf{k}.\mathbf{x}'} d\mathbf{x}' \right)
\end{aligned}$$

But $u(\varphi) e^{i\mathbf{k}.\mathbf{x}'} = u(\varphi) e^{i\mathbf{k}.\mathbf{x}} e^{i\mathbf{k}.(\mathbf{x}' - \mathbf{x})}$. If we factor out $e^{i\mathbf{k}.\mathbf{x}}$ and note that

$$\int_R w_{lat}(\mathbf{x} - \mathbf{x}', \varphi + \psi) e^{i\ \mathbf{k}.(\mathbf{x}' - \mathbf{x})} d\mathbf{x}' = \tilde{w}_{lat}(\mathbf{k}, \varphi + \psi)$$

is the Fourier transform of w_{lat} w.r.t. the spatial variables $\mathbf{x}$, we get

$$\lambda u(\varphi) = -\alpha u(\varphi) + \sigma'(0)\mu \left(\int_0^{\pi} w_{loc}(\varphi - \varphi') u(\varphi') \frac{d\varphi'}{\pi} \right) \tag{16}$$

$$+\sigma'(0)\mu\beta \tilde{w}_{lat}(\mathbf{k}, \varphi + \psi) u(\varphi). \tag{17}$$

The $E(2)$-symmetry imposes very strong constraints on the phase functions $u(\varphi)$.

Let $u(\varphi) = \sum_{n \in \mathbb{Z}} U_n e^{2in\varphi}$ and $w_{loc}(\varphi) = \sum_{n \in \mathbb{Z}} W_{loc,n} e^{2in\varphi}$ be the Fourier series of the periodic functions $u(\varphi)$ and $w_{loc}(\varphi)$.

As $w_{loc}(\varphi)$ is an even real function, $W_{loc,-n} = \overline{W_{loc,n}} = W_{loc,n}$.

If $u(\varphi)$ is an *even* function, $U_{-n} = U_n$, if $u(\varphi)$ is an *odd* function, $U_{-n} = -U_n$.

From equation (16) we get:

$$\lambda \left(\sum_{m\in\mathbb{Z}} U_m e^{2im\varphi} \right) = -\alpha \left(\sum_{m\in\mathbb{Z}} U_m e^{2im\varphi} \right)$$
$$+\sigma'(0)\mu \left(\int_0^\pi \left(\sum_{n\in\mathbb{Z}} W_{loc,n} e^{2in(\varphi-\varphi')} \right) \left(\sum_{m\in\ \mathbb{Z}} U_m e^{2im\varphi'} \right) \frac{d\varphi'}{\pi} \right)$$
$$+\sigma'(0)\mu\beta \left(\int_R w_{lat}(\mathbf{x}',\varphi+\psi) e^{-i\mathbf{k}.\mathbf{x}'} d\mathbf{x}' \right) \left(\sum_{m\in\mathbb{Z}} U_m e^{2im\varphi} \right).$$

In the second term of the rhs, $\int_0^\pi e^{2i(m-n)\varphi'} \frac{d\varphi'}{\pi} = \delta_{m,n}$ and for $m = n$ it remains only the factor $e^{2im\varphi}$ of $e^{2i(n=m)(\varphi-\varphi')}$.

Hence, the second term $= \sigma'(0)\mu \left(\sum_{m\in\mathbb{Z}} W_{loc,m} U_m e^{2im\varphi} \right)$.

For the third term of the rhs, we make a rotation of $\varphi + \psi$ in $\int_R w_{lat}(\mathbf{x}',\varphi+\psi) e^{-i\mathbf{k}.\mathbf{x}'} d\mathbf{x}'$ and we get $\int_R w_{lat}(\mathbf{x}',0) e^{-i\mathbf{k}.r_{\varphi+\psi}(\mathbf{x}')} d\mathbf{x}'$.

We use $\sum_{n\in\mathbb{Z}} \left(\int_0^\pi e^{-2i(m-n)\varphi} \frac{d\varphi}{\pi} \right) = \delta_{m,n}$ and put

$$\hat{W}_{lat,n}(q) = \int_0^\pi e^{-2in\varphi'} \left(\int_R w_{lat}(\mathbf{x},0) e^{-i\mathbf{k}.r_\varphi(\mathbf{x})} d\mathbf{x} \right) \frac{d\varphi'}{\pi}$$

which is a coefficient depending only on the module $q = |\mathbf{k}|$ of the wave vector $\mathbf{k}$.

As $w_{lat}(\mathbf{x},0)$ is an even function of $\mathbf{x}$, $\hat{W}_{lat,-n}(q) = \hat{W}_{lat,n}(q)$.

In terms of the $\hat{W}_{lat,n}(q)$ the third term =

$$\sigma'(0)\mu\beta \left(\int_R w_{lat}(\mathbf{x}',\varphi+\psi) e^{-i\mathbf{k}.\mathbf{x}'} d\mathbf{x}' \right) \left(\sum_{m\in\mathbb{Z}} \sum_{n\in\mathbb{Z}} \int_0^\pi e^{-2i(m-n)\varphi'} U_n e^{2im\varphi} \frac{d\varphi'}{\pi} \right)$$
$$= \sigma'(0)\mu\beta \sum_{m\in\mathbb{Z}} \sum_{n\in\mathbb{Z}} \left(\int_R w_{lat}(\mathbf{x}',\varphi+\psi) e^{-i\mathbf{k}.\mathbf{x}'} d\mathbf{x}' \right) \left(\int_0^\pi e^{-2i(m-n)\varphi'} U_n e^{2im\varphi} \frac{d\varphi'}{\pi} \right)$$
$$= \sigma'(0)\mu\beta \sum_{m\in\mathbb{Z}} \sum_{n\in\mathbb{Z}} \int_0^\pi e^{-2i(m-n)\varphi'} \left(\int_R w_{lat}(\mathbf{x}',\varphi+\psi) e^{-i\mathbf{k}.\mathbf{x}'} d\mathbf{x}' \right) \frac{d\varphi'}{\pi} \left(U_n e^{2im\varphi} \right)$$
$$= \sigma'(0)\mu\beta \sum_{m\in\mathbb{Z}} \sum_{n\in\mathbb{Z}} \hat{W}_{lat,m-n}(q) U_n e^{2im\varphi}.$$

If we identify the coefficients of $e^{2im\varphi}$ in the lhs and the rhs we get dispersion relations:

$$\lambda U_m = -\alpha U_m + \sigma'(0)\mu W_{loc,m} U_m + \sigma'(0)\mu\beta \sum_{n\in\mathbb{Z}} \hat{W}_{lat,m-n}(q) U_n$$

which can be writen

$$\left(\frac{\lambda+\alpha}{\sigma'(0)\mu} - W_{loc,m}\right) U_m = \beta \sum_{n\in\mathbb{Z}} \hat{W}_{lat,m-n}(q) U_n. \tag{18}$$

Now the solutions must be invariant with respect to the reflexion κ through $\mathbf{k}$ (κ leaves $\mathbf{k}$ invariant). But

$$\kappa a(\mathbf{x},\varphi) = a(\kappa\mathbf{x}, 2\psi - \varphi) = u(2\psi - \varphi - \psi)e^{i\mathbf{k}.\kappa\mathbf{x}} = u(\psi - \varphi)e^{i\mathbf{k}.\mathbf{x}}$$

and, since $\kappa^2 = 1$, u must be an *even* or an *odd* function.

7 Weak lateral anisotropy and β-developments

It is an experimental fact that horizontal connections are *weak* relative to the vertical ones.

We use developments in β.

7.1 Case $\beta = 0$

$\beta = 0$. Model without lateral connections (“ ring model ”).

Dispersion relation: $\lambda = -\alpha + \sigma'(0)\mu W_{loc,m}$.

To get a *stationnary* solution we must have $\lambda = 0$ that is $-\alpha + \sigma'(0)\mu W_{loc,m} = 0$.

As α, $\sigma'(0)$ and $W_{loc,m}$ are given, each of these equations defines a *critical value*

$$\mu_c = \frac{\alpha}{\sigma'(0)W_{loc,m}}.$$

As $W_{loc,-m} = W_{loc,m}$, this will select m and $-m$ and excite linear modes of the form

$$a(\mathbf{x}, \varphi) = z_m(\mathbf{x})e^{2im\varphi} + c.c$$

First critical value $\mu_c = \frac{\alpha}{\sigma'(0)W_{loc,p}}$ for $W_{loc,p} = \max(W_{loc,m})$.

If $z_p(\mathbf{x}) = \rho(\mathbf{x})e^{2i\theta(\mathbf{x})}$, $a(\mathbf{x}, \varphi) = 2\rho(\mathbf{x})\cos(2(p\varphi + \theta(\mathbf{x})))$.

The activity is maximal for $\cos = 1$, that is for $2(p\varphi + \theta(\mathbf{x})) = 2l\pi$ or $\varphi = -\theta(\mathbf{x}) + \frac{l\pi}{p}$.

1. If $p = 1$ (unimodal orientation tuning curves), unique solution $\varphi = -\theta(\mathbf{x})$ and we get a *local contour*:

   > “ a sharply tuned response at some angle $-\theta(\mathbf{x})$ in a local region of $V1$ ” (Bressloff)

   Due to the lack of horizontal connections these local contours are decorrelated.

2. If $p = 0$ there is a bulk instability $\Longrightarrow$ stationnary states $a(\mathbf{x}, \varphi) = a(\mathbf{x}) = 2\rho(\mathbf{x})\cos(2\theta(\mathbf{x})) = z_0(\mathbf{x}) + \overline{z_0(\mathbf{x})}$ without any preferential orientation.

7.2 Perturbative developments in β (case $p = 1$)

$\beta > 0$. We use perturbative developments of the case $\beta = 0$ where

$$\frac{\lambda + \alpha}{\sigma'(0)\mu} = W_{loc,1}$$

and $a(\mathbf{x}, \varphi) = z_{\pm 1}(\mathbf{x}) e^{\pm 2i\varphi}$ i.e. $U_n = z_{\pm 1}(\mathbf{x})\delta_{n,\pm 1}$.
We take again the dispersion relations

$$\left(\frac{\lambda + \alpha}{\sigma'(0)\mu} - W_{loc,m} \right) U_m = \beta \left(\sum_{n \in \mathbb{Z}} \hat{W}_{lat,m-n}(q) U_n \right)$$

and we expand $\frac{\lambda+\alpha}{\sigma'(0)\mu}$ and U_n starting from their values for $\beta = 0$:

$$\begin{aligned} \frac{\lambda + \alpha}{\sigma'(0)\mu} &= W_{loc,1} + \beta\lambda^{(1)} + \beta^2\lambda^{(2)} + \ldots \\ U_n &= z_{\pm 1}(\mathbf{x})\delta_{n,\pm 1} + \beta U_n^{(1)} + \beta^2 U_n^{(2)} + \ldots \end{aligned}$$

The dispersion relations become:

$$\begin{aligned} & \left(W_{loc,1} + \beta\lambda^{(1)} + \beta^2\lambda^{(2)} + \ldots - W_{loc,m} \right) \\ & \left(z_{\pm 1}(\mathbf{x})\delta_{m,\pm 1} + \beta U_m^{(1)} + \beta^2 U_m^{(2)} + \ldots \right) \\ = & \beta \left(\sum_{n \in \mathbb{Z}} \hat{W}_{lat,m-n}(q) \left(z_{\pm 1}(\mathbf{x})\delta_{n,\pm 1} + \beta U_n^{(1)} + \beta^2 U_n^{(2)} + \ldots \right) \right). \end{aligned}$$

and identifying the coefficients of the successive powers of β in lhs and rhs leads to equations for $z_{\pm 1}(\mathbf{x})$ and $U_n^{(j)}$.

7.3 Unstability and bifurcations

Using Fourier series, Fourier transforms and β-developments, we get some idea of the form of the phase functions $u(\varphi)$ in the solutions of the form $a(\mathbf{x},\varphi) = u(\varphi-\psi)e^{i\mathbf{k}.\mathbf{x}} + c.c.$ We want now to analyse further the stability of these solutions using the β-developments of the eigenvalues in the dispersion relations (18):

$$\begin{aligned}\frac{\lambda_\pm + \alpha}{\sigma'(0)\mu} \simeq & W_{loc,1} + \beta\left(\hat{W}_{lat,0}(q) \pm \hat{W}_{lat,2}(q)\right) \\ & +\beta^2\left(\sum_{n\in\mathbb{N},n\neq 1} \frac{\left(\hat{W}_{lat,1-n}(q) \pm \hat{W}_{lat,1+n}(q)\right)^2}{W_{loc,1} - W_{loc,n}}\right) \\ = & G_\pm(q)\end{aligned}$$

Best situation: $G_\pm(q)$ has a unique maximum q_c.

The homogeneous solution $a(\mathbf{x},\varphi)$ will become unstable when $\lambda_\pm$ crosses the 0 value, that is for the critical value μ_c

$$\mu_c = \frac{\alpha}{\sigma'(0)G_\pm(q_c)}$$

When μ crosses the critical value μ_c, some eigenmodes are activated and we get solutions of the type:

$$a(\mathbf{x},\varphi) = \sum_{j=1}^{j=N} c_j u(\varphi-\psi_j)e^{i\mathbf{k}_j.\mathbf{x}} + c.c.$$

with $\mathbf{k}_j = q_c\left(\cos\left(\psi_j\right), \sin\left(\psi_j\right)\right)$ and $u(\varphi-\psi_j) = u^\pm(\varphi-\psi_j)$ and the form of u contrained by the previous computations of β-developments.

Fundamental difficulty: due to rotation invariance, the degeneracy degree of the eigenvalue is *infinite*; *all* the modes sharing wave vectors $\mathbf{k}$ with the same wavelength q_c become unstable together.

It is necessary to reduce the solutions to *finite* linear superpositions of eigenmodes.

It is here that the authors introduce their main hypothesis.

8 Planforms and symmetry breaking

8.1 The double periodicity hypothesis

The authors suppose that the solutions are *spatially doubly periodic* relative to a lattice $\mathcal{L}$ of R.

This heuristic hypothesis is justified:

1. by the experimental validity of its results,
2. by the fact that it is widely verified in fluid dynamics, chemical reaction-diffusion processes, etc. for many bifurcations due to symmetry-breaking.

The solutions restricted by this double periodicity constraint are called *planforms*. They are well known and

> " There is a common approach to all lattice bifurcation problems " (Bressloff *et al.*)

8.2 Lattices

The authors work in three lattices of the plane R: $\mathcal{L} = \{2\pi m_1 \mathbf{l}_1 + 2\pi m_2 \mathbf{l}_2\}$ $(m_1, m_2 \in \mathbb{Z})$ and their dual lattices $\mathcal{L}^*$ generated by the wave vectors $\mathbf{k}_1, \mathbf{k}_2$ such that $\mathbf{l}_i.\mathbf{k}_j = \delta_{ij}$.

If $\mathbf{k} \in \mathcal{L}^*$, the plane wave $e^{i\mathbf{k}.\mathbf{x}}$ is $\mathcal{L}$-periodic.

	$\mathbf{l}_1$	$\mathbf{l}_2$	$\mathbf{k}_1$	$\mathbf{k}_2$
Square	$(1,0)$	$(0,1)$	$(1,0)$	$(0,1)$
Hexagonal	$\left(1, \frac{1}{\sqrt{3}}\right)$	$\left(0, \frac{2}{\sqrt{3}}\right)$	$(1,0)$	$\frac{1}{2}\left(-1, \sqrt{3}\right)$
Rhombic	$(1, -\cot\eta)$	$(0, \frac{1}{\sin\eta}$	$(1,0)$	$(\cos\eta, \sin\eta)$

where, in the rhombic case, $\eta \neq 0, \frac{\pi}{3}, \frac{\pi}{2}$.

The main advantage to restrict to a lattice $\mathcal{L}$ is that the *non compact* Euclidean group $E(2)$ is reduced to the *compact* symmetry group

$$\Gamma_{\mathcal{L}} = H_{\mathcal{L}} \dot{+} T^2$$

where:

1. $H_{\mathcal{L}}$ is the *holohedry group* of $\mathcal{L}$ = the subgroup of rotations and reflexions of $O(2)$ preserving $\mathcal{L}$,
2. T^2 is the 2-*torus* $\mathbb{R}^2/\mathcal{L}$.

The holohedry groups are *dihedral groups*: D_n is the group of order $2n$ generated by a rotation ξ of order n and a reflexion κ.

The reflexion κ is the symmetry around the x-axis $\mathbf{k}_1 \to \mathbf{k}_1$, $\mathbf{k}_2 \to -\mathbf{k}_2$ for the square and hexagonal cases and is the exchange of $\mathbf{k}_1$ and $\mathbf{k}_2$ for the rhombic case.

The rotation ξ is $\frac{\pi}{2}$ for the square lattice, $\frac{\pi}{3}$ for the hexagonal one, and π for the rhombic one.

We have always $\xi\kappa = \kappa\xi^{-1}$.

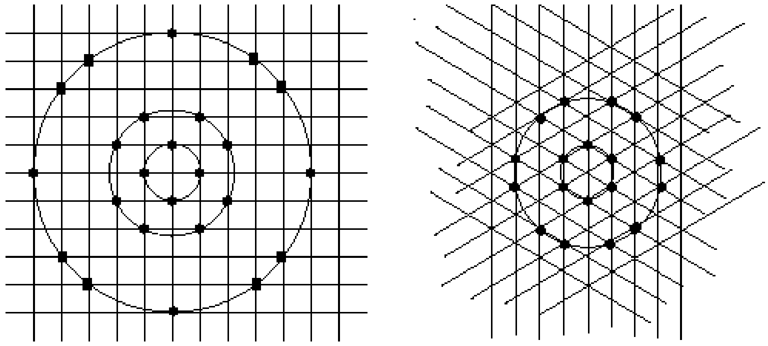


Figure 4: Minimal and non minimal length wave vectors.

8.3 Spaces of solutions

Simplest case: the *critical* wave vectors are of *minimal length* $q_c = 1$. This hypothesis is very strong:

We are led to study $\mathbb{C}$-linear superpositions of solutions $u(\varphi-\psi)e^{i\ \mathbf{k}.\mathbf{x}}+$ *c.c.*. They generate a functional space $\mathcal{F}$.

We study solutions of the type

$$\begin{cases} \mathcal{L} \text{ square} & c_1 u(\varphi)e^{i\mathbf{k}_1.\mathbf{x}} + c_2 u\left(\varphi - \frac{\pi}{2}\right) e^{i\mathbf{k}_2.\mathbf{x}} + c.c. \\ \mathcal{L} \text{ hexagonal} & \begin{cases} c_1 u(\varphi)e^{i\mathbf{k}_1.\mathbf{x}} + c_2 u\left(\varphi - \frac{2\pi}{3}\right) e^{i\mathbf{k}_2.\mathbf{x}} \\ +c_3 u\left(\varphi + \frac{4\pi}{3}\right) e^{i\mathbf{k}_3.\mathbf{x}} + c.c. \\ \text{with } \mathbf{k}_3 = -\left(\mathbf{k}_1 + \mathbf{k}_2\right) \end{cases} \\ \mathcal{L} \text{ rhombic} & c_1 u(\varphi)e^{i\mathbf{k}_1.\mathbf{x}} + c_2 u(\varphi - \eta)e^{i\mathbf{k}_2.\mathbf{x}} + c.c. \end{cases}$$

where $u(\varphi)$ is an *even* or an *odd* function.

We work now directly *on the coordinates* c_i of $\mathcal{K}$ and compute the action of $\Gamma_{\mathcal{L}}$ on them.

8.4 The group action on the coordinates of $\mathcal{K}$

8.4.1 Example: the square case

Action of the translations T^2. Let $2\pi\tau = (2\pi\tau_1\mathbf{l}_1 + 2\pi\tau_2\mathbf{l}_2) \in T^2$ ($\tau_1, \tau_2 \in [0, 1[$) . We note it $\tau = [\tau_1, \tau_2]$. It acts as $\tau\left(u(\varphi)e^{i\mathbf{k}.\mathbf{x}}\right) = u(\varphi)e^{i\mathbf{k}.(\mathbf{x}-2\pi\tau)} = e^{-2i\pi\mathbf{k}.\tau}u(\varphi)e^{i\mathbf{k}.\mathbf{x}}$ and therefore

$$\begin{cases} \mathcal{L} \text{ square} & [\tau_1, \tau_2]\,(c_1, c_2) = (e^{-2i\pi\tau_1}c_1, e^{-2i\pi\tau_2}c_2) \\ \mathcal{L} \text{ hexagonal} & [\tau_1, \tau_2]\,(c_1, c_2, c_3) = \left(e^{-2i\pi\tau_1}c_1, e^{-2i\pi\tau_2}c_2, e^{2i\pi(\tau_1+\tau_2)}c_3\right) \\ \mathcal{L} \text{ rhombic} & [\tau_1, \tau_2]\,(c_1, c_2) = (e^{-2i\pi\tau_1}c_1, e^{-2i\pi\tau_2}c_2)\,. \end{cases}$$

Action of the holohedry $H_{\mathcal{L}} = D_4(\xi, \kappa)$.

$$\begin{aligned} \xi\,(c_1, c_2) &= r_{\frac{\pi}{2}}\left(c_1u(\varphi)e^{i\mathbf{k}_1.\mathbf{x}} + c_2u\left(\varphi - \frac{\pi}{2}\right)e^{i\mathbf{k}_2.\mathbf{x}} + c.c.\right) \\ &= c_1u\left(\varphi - \frac{\pi}{2}\right)e^{ir_{\frac{\pi}{2}}(\mathbf{k}_1).\mathbf{x}} + c_2u\left(\varphi - \pi\right)e^{ir_{\frac{\pi}{2}}(\mathbf{k}_2).\mathbf{x}} + c.c. \\ &= c_1u\left(\varphi - \frac{\pi}{2}\right)e^{i\mathbf{k}_2.\mathbf{x}} + c_2u\left(\varphi\right)e^{-i\mathbf{k}_1.\mathbf{x}} + c.c. \\ &= (\overline{c_2}, c_1) \end{aligned}$$

where in the last equality we exchanged $c_2u(\varphi)\,e^{-i\mathbf{k}_1.\mathbf{x}}$ and its complex conjugate $\overline{c_2}u(\varphi)\,e^{i\mathbf{k}_1.\mathbf{x}}$ to get an $u(\varphi)\,e^{i\mathbf{k}_1.\mathbf{x}}$ component.

As for the reflexion κ, it acts as $\mathbf{k}_1 \to \mathbf{k}_1$, $\mathbf{k}_2 \to -\mathbf{k}_2$, and $\varphi \to -\varphi$. Then:

$$\begin{aligned} \kappa\,(c_1, c_2) &= \kappa\left(c_1u(\varphi)e^{i\mathbf{k}_1.\mathbf{x}} + c_2u\left(\varphi - \frac{\pi}{2}\right)e^{i\mathbf{k}_2.\mathbf{x}} + c.c.\right) \\ &= c_1u\left(-\varphi\right)e^{i\mathbf{k}_1.\mathbf{x}} + c_2u\left(-\varphi + \frac{\pi}{2}\right)e^{-i\mathbf{k}_2.\mathbf{x}} + c.c. \\ &= \pm c_1u\left(\varphi\right)e^{i\mathbf{k}_1.\mathbf{x}} \pm \overline{c_2}u\left(\varphi - \frac{\pi}{2}\right)e^{i\mathbf{k}_2.\mathbf{x}} + c.c. \\ &= \pm\left(c_1, \overline{c_2}\right) \text{ according to the even/odd case for } u. \end{aligned}$$

We know therefore the action of $\Gamma_{\mathcal{L}} = D_4 \dot{+} T^2$ on $\mathcal{K} \simeq \mathbb{C}^2$:

$1\,(c_1, c_2) = (c_1, c_2)$,
$\xi\,(c_1, c_2) = (\overline{c_2}, c_1)$,
$\xi^2\,(c_1, c_2) = (\overline{c_1}, \overline{c_2})$,
$\xi^3\,(c_1, c_2) = (c_2, \overline{c_1})$,
$\kappa\,(c_1, c_2) = \pm\,(c_1, \overline{c_2})$,
$\kappa\xi\,(c_1, c_2) = \pm\,(\overline{c_2}, \overline{c_1})$,
$\kappa\xi^2\,(c_1, c_2) = \pm\,(\overline{c_1}, c_2)$,
$\kappa\xi^3\,(c_1, c_2) = \pm\,(c_2, c_1)$,
$[\tau_1, \tau_2]\,(c_1, c_2) = (e^{-2i\pi\tau_1}c_1, e^{-2i\pi\tau_2}c_2)$.

See the text for the other cases.
To analyse the bifurcations we use a fundamental tool.

9 The application of Golubitsky's equivariant branching lemma

Let Γ be a group acting on a $\mathbb{R}$-vector space $\mathcal{K}$ and let Σ be a subgroup of Γ. We note $\mathrm{Fix}\,(\Sigma)$ the subset of $\mathcal{K}$ fixed by Σ (Σ is the *isotropy subgroup* of $\mathrm{Fix}\,(\Sigma)$) and we say that Σ is *axial* if $\mathrm{Fix}\,(\Sigma)$ is of dimension 1.

Equivariant Branching Lemma. Let Γ be a Lie group acting in a way absolutely irreducible on $\mathcal{K}$ (that is the linear maps commuting with the action of Γ are scalar multiples of the identity) and let $F \in \mathcal{E}(\Gamma)$ (where $\mathcal{E}(\Gamma)$ is the space of Γ-equivariant germs at the origin 0 of C^∞ mappings of $\mathcal{K}$ into $\mathcal{K}$) be a bifurcation problem (depending on a bifurcation parameter λ) with symmetry group Γ. Let Σ be an axial isotropy subgroup ($\dim \mathrm{Fix}(\Sigma) = 1$). Then there exists a unique smooth solution branch to $F = 0$ such that the isotropy subgroup of each solution is Σ.

9.1 Case $\mathcal{L}$ square, $u(\varphi)$ even

Let $(c_1, c_2) \in \mathcal{K} = \mathbb{C}^2$. Using the T^2 action $[\tau_1, \tau_2](c_1, c_2) = (e^{-2i\pi\tau_1} c_1, e^{-2i\pi\tau_2} c_2)$ we may suppose that $c_1, c_2 \in \mathbb{R}^+$. We look at the isotropy group Σ of (c_1, c_2) and we ask if it is axial.

If $c_1 > 0$, $c_2 > 0$, $[\tau_1, \tau_2]$ must be $[0, 0]$ to fix (c_1, c_2). For the dihedral group D_4,

$1\,(c_1, c_2) = (c_1, c_2)$,
$\xi\,(c_1, c_2) = (c_2, c_1)$,
$\xi^2\,(c_1, c_2) = (c_1, c_2)$,
$\xi^3\,(c_1, c_2) = (c_2, c_1)$,
$\kappa\,(c_1, c_2) = (c_1, c_2)$,
$\kappa\xi\,(c_1, c_2) = (c_2, c_1)$,
$\kappa\xi^2\,(c_1, c_2) = (c_1, c_2)$,
$\kappa\xi^3\,(c_1, c_2) = (c_2, c_1)$.

The subgroup $\Sigma = \left\{1, \xi^2, \kappa, \kappa\xi^2\right\} = D_2\left(\xi^2, \kappa\right)$ fixes all the (c_1, c_2) real and $\dim \mathrm{Fix}(\Sigma) = 2$. It is not axial.

But if $c_1 = c_2$, the subgroup $\Sigma = D_4(\xi, \kappa)$ fixes the diagonal which is of $\dim \mathrm{Fix}(D_4) = 1$. The subgroup D_4 is therefore *axial* and there will be a bifurcating branch of planforms (eigenfunctions) called *Even Squares*:

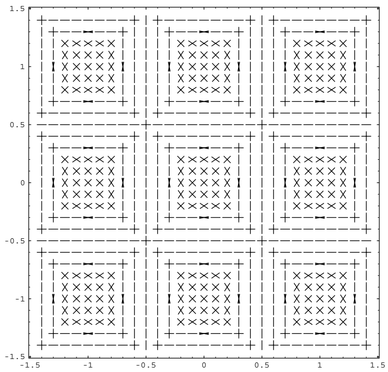
$$
\begin{aligned}
a(\mathbf{x}, \varphi) &= u(\varphi)\cos(\mathbf{k}_1.\mathbf{x}) + u\left(\varphi - \frac{\pi}{2}\right)\cos(\mathbf{k}_2.\mathbf{x}) \\
&= u(\varphi)\cos(x) + u\left(\varphi - \frac{\pi}{2}\right)\cos(y)
\end{aligned}
$$

Computation of a case $u(\varphi)$ even given by the previous computations: $u(\varphi) = \cos(2\varphi) - 0.5\cos(4\varphi)$ which vanishes for $x^\circ = y^\circ = \frac{1}{4}$ ($x = 2\pi x^\circ$, $y = 2\pi y^\circ$).

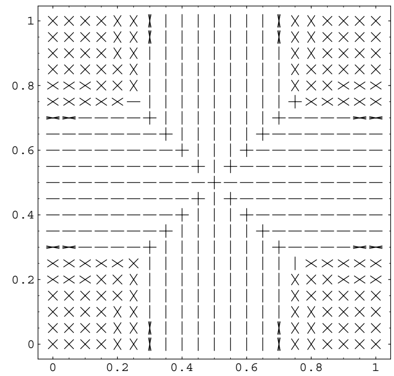
Fundamental domain: $x^\circ, y^\circ \in \left[0, \frac{1}{2}\right]$. We show (Table 4.1) the φ for which $a(\mathbf{x}, \varphi)$ is maximal and a zoom on the domain.

In Table 5: family of graphs of $a(\mathbf{x}, \varphi)$ for $\mathbf{x}^\circ \in \left[0, \frac{1}{2}\right] \times \{0\}$, $\{0\} \times \left[0, \frac{1}{2}\right]$, $\left[0, \frac{1}{2}\right] \times \left[0, \frac{1}{2}\right]$.

In Table 6: graphs of $a(\mathbf{x}, \varphi)$ for the nine points $\mathbf{x}^\circ \in \left\{\frac{1}{8}, \frac{1}{4}, \frac{3}{8}\right\} \times \left\{\frac{1}{8}, \frac{1}{4}, \frac{3}{8}\right\}$.

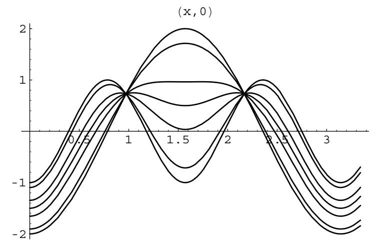


1. Even squares.

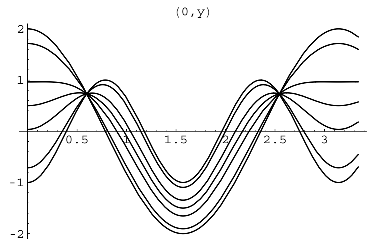


2. Zoom on the even squares.

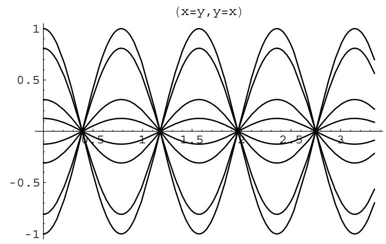
Table 4



$\mathbf{x}^\circ \in \left[0, \frac{1}{2}\right] \times \{0\}$



$\mathbf{x}^\circ \in \{0\} \times \left[0, \frac{1}{2}\right]$



$\mathbf{x}^\circ \in \mathrm{Diag}\left(\left[0, \frac{1}{2}\right] \times \left[0, \frac{1}{2}\right]\right)$

Table 5: Families of graphs of the phase functions $a(\mathbf{x}, \varphi)$.

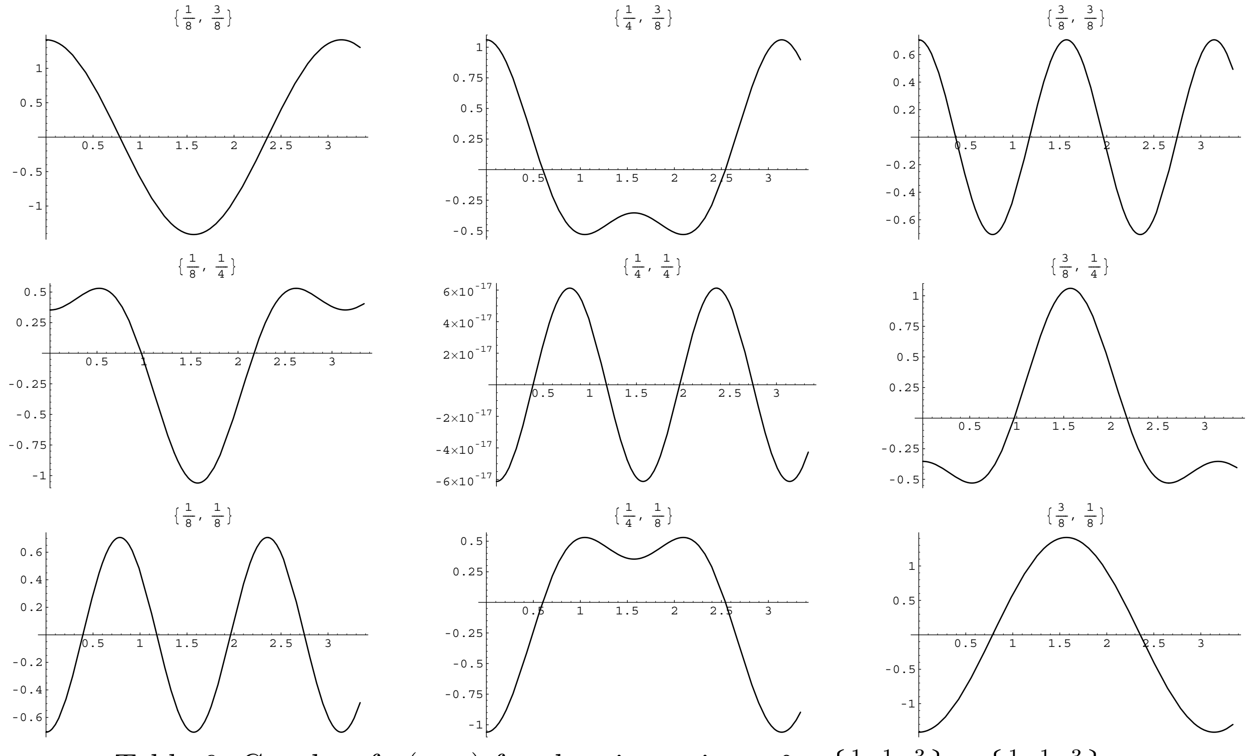


Table 6: Graphs of $a(\mathbf{x}, \varphi)$ for the nine points $\mathbf{x}^\circ \in \left\{\frac{1}{8}, \frac{1}{4}, \frac{3}{8}\right\} \times \left\{\frac{1}{8}, \frac{1}{4}, \frac{3}{8}\right\}$.

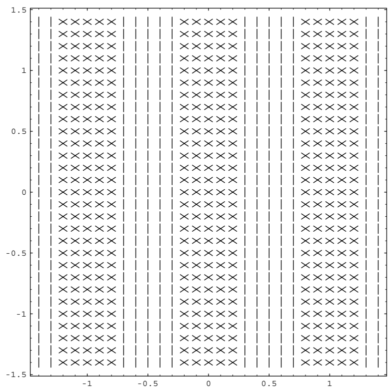


Figure 5: Even rolls

If $c_1 > 0$, $c_2 = 0$ (or vice-versa), τ_1 must be $= 0$, but τ_2 can have *any* value. The isotropy holohedric subgroup is the dihedral subgroup $D_2\left(\xi^2, \kappa\right)$. The total isotropy subgroup $D_2\left(\xi^2, \kappa\right) \dotplus S^1(\tau_2)$ is *axial* and correspond to a bifurcating branch of planforms called *Even Rolls*:

$$a(\mathbf{x}, \varphi) = u(\varphi)\cos(\mathbf{k}_1.\mathbf{x}) = u(\varphi)\cos(x)$$

If $c_1 = 0$, $c_2 = 0$, the orbit is $\{0\}$ and the isotropy group is the total group $\Gamma_{\mathcal{L}}$ which is not axial.

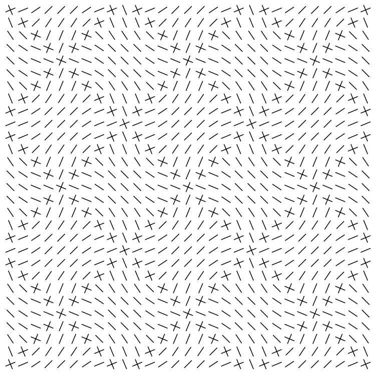


Figure 6: Odd squares

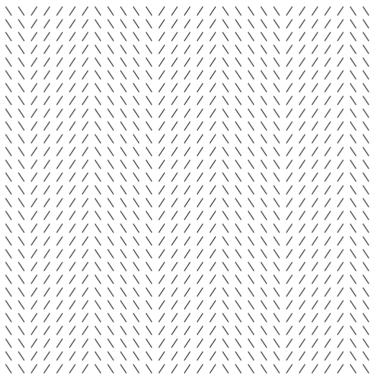


Figure 7: Odd rolls

9.2 Case $\mathcal{L}$ square, $u(\varphi)$ odd

If $c_1 > 0$, $c_2 > 0$, $c_1 = c_2$ $(= 1)$ *Odd Squares.*

$$\begin{aligned} a(\mathbf{x}, \varphi) &= u(\varphi) \cos(\mathbf{k}_1.\mathbf{x}) + u\left(\varphi - \frac{\pi}{2}\right) \cos(\mathbf{k}_2.\mathbf{x}) \\ &= u(\varphi) \cos(x) + u\left(\varphi - \frac{\pi}{2}\right) \cos(y) \end{aligned}$$

If $c_1 > 0$, $c_2 = 0$ (or vice-versa), *Odd Rolls*:

$$a(\mathbf{x}, \varphi) = u(\varphi) \cos(\mathbf{k}_1.\mathbf{x}) = u(\varphi) \cos(x).$$

9.3 Non-contoured planforms

There are also *non-contoured* plaforms which can be approximated by $u(\varphi) \simeq 1$ and are independent of the phase φ: $a(\mathbf{x}, \varphi) = a(\mathbf{x})$

1. Square

$$a(\mathbf{x}) = \cos(\mathbf{k}_1.\mathbf{x}) + \cos(\mathbf{k}_2.\mathbf{x}) = \cos(x) + \cos(y).$$

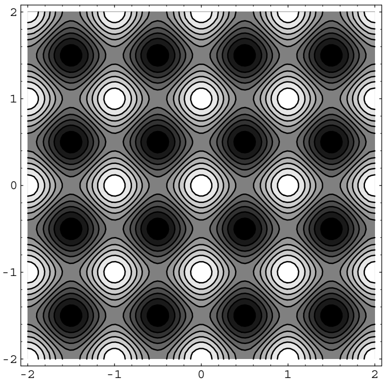
2. Hexagonal

$$\begin{aligned} a(\mathbf{x}) &= \cos\left(\mathbf{k}_1.\mathbf{x}\right) + \cos\left(\mathbf{k}_2.\mathbf{x}\right) + \cos\left(\mathbf{k}_3.\mathbf{x}\right) \\ &= \cos\left(x\right) + \cos\left(-\frac{\mathbf{x}}{2} + \frac{\sqrt{3}}{2}y\right) + \cos\left(-\frac{\mathbf{x}}{2} - \frac{\sqrt{3}}{2}y\right). \end{aligned}$$

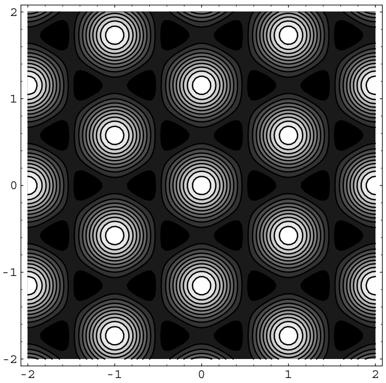
3. Rhombic

$$\begin{aligned} a(\mathbf{x}) &= \cos(\mathbf{k}_1.\mathbf{x}) + \cos(\mathbf{k}_2.\mathbf{x}) \\ &= \cos(x) + \cos\left(x\cos(\eta) + y\sin(\eta)\right) \end{aligned}$$

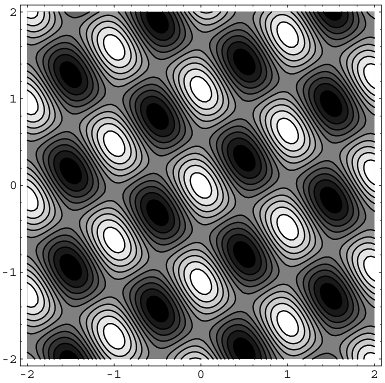
Contour plot at Table 9 for $\mathbf{x}^\circ \in [-2, 2] \times [-2, 2]$.



1. Non-contoured squares.



2. Non-contoured hexagons.



3. Non-contoured rhombs.

Table 9

The plot can be made binary by a simple *thresholding*.

9.4 Simplified representations of planforms

The planforms $a(\mathbf{x}, \varphi)$ are functions on a fibration $R \times S^1 \to R$. They can be considered as phase functions $a_{\mathbf{x}}(\varphi)$ of the angular variable φ (the fiber S^1) controled by the space variable $\mathbf{x}$ (the base space R). They can present "catastrophes".

We consider the maxima of $a_{\mathbf{x}}(\varphi)$ and plot them at the center of regular zones.

Case $\mathcal{L}$ square and $u(\varphi)$ = the even function $\cos(2\varphi)$ (Table 9. 1).

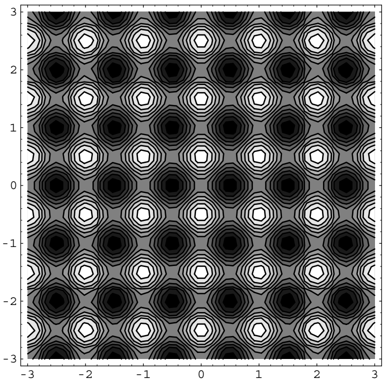
$$\begin{aligned} a(\mathbf{x}, \varphi) &= \cos(2\varphi)\cos(x) + \cos(2\varphi - \pi)\cos(y) \\ &= -2\cos(2\varphi)\sin\left(\frac{x-y}{2}\right)\sin\left(\frac{x+y}{2}\right) \end{aligned}$$

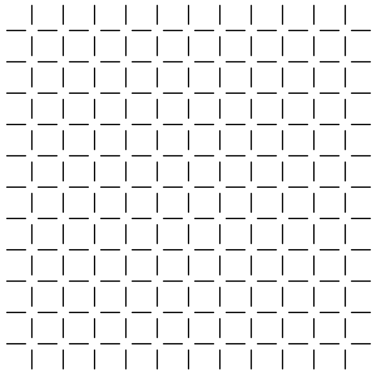
The phase factor $\cos(2\varphi)$ is maximal $= 1$ for $\varphi = 0$ and minimal $= -1$ for $\varphi = \frac{\pi}{2}$.

The space factor $-2\sin\left(\frac{x-y}{2}\right)\sin\left(\frac{x+y}{2}\right)$ vanishes for $x - y = 2k$ and $x + y = 2l$ (Table 9.1).

We get a diagonal chessboard and at the center of the cells the maximum of $a(\mathbf{x}, \varphi)$ is given by $\varphi = 0$ or $\varphi = \frac{\pi}{2}$.

Hence the simplified representation in Table 9.2.

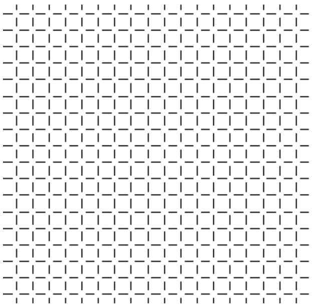




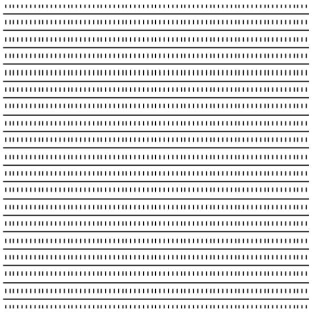
1. Contour plot of simple even squares. 2. Simplified plot of simple even squares.

Table 9

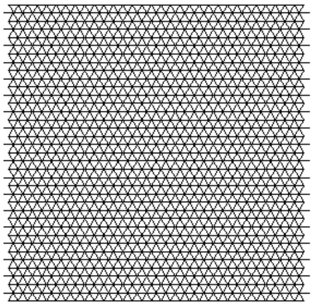
The authors give simplified representations of the planforms (tables 10, 11, 12).



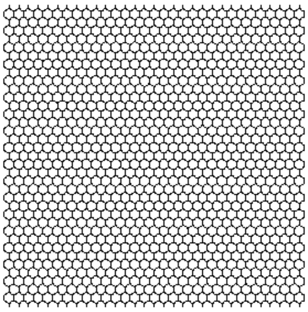
1. Even squares.



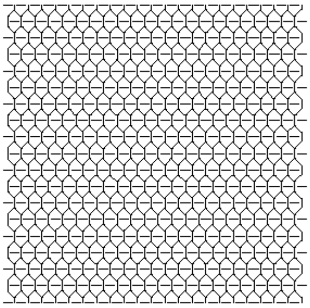
2. Even rolls.



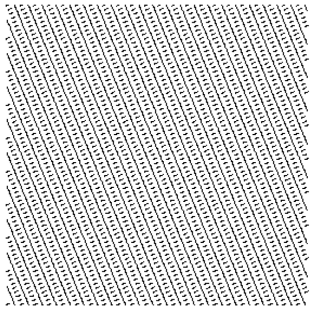
3. Even hexagons I.



4. Even Hexagons II.

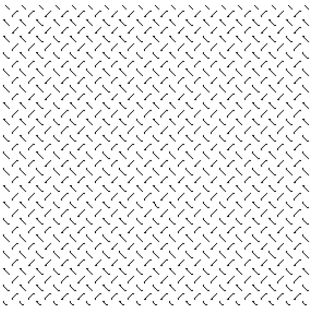


5. Even rhombs.

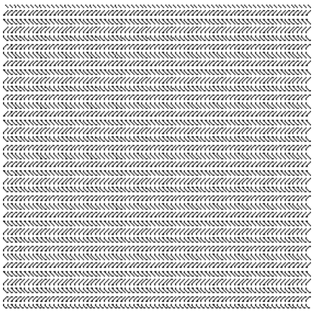


6. Even rhombic rolls.

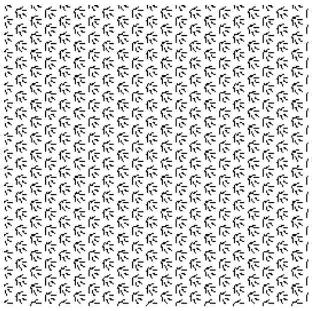
Table 10



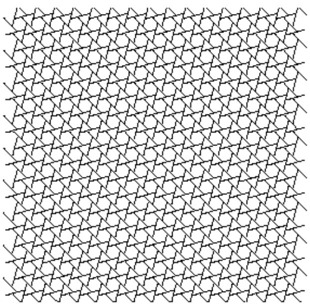
1. Odd squares.



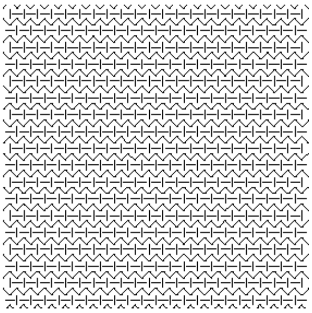
2. Odd rolls.



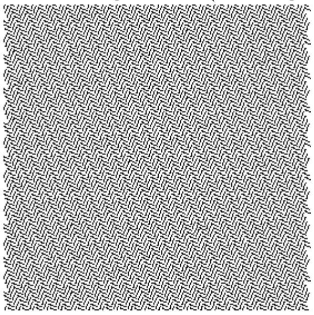
3. Odd hexagons I (triangles).



4. Odd hexagons II.

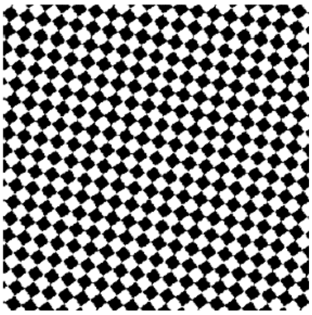


5. Odd rhombs.

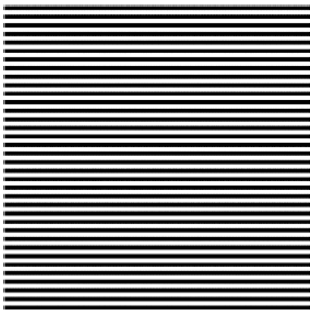


6. Odd rhombic rolls.

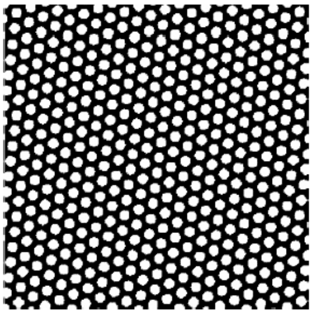
Table 11



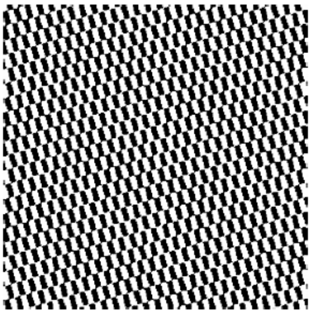
1. Non-contoured squares.



2. Non-contoured rolls.



3. Non-contoured hexagons.



4. Non-contoured rhombs.

Table 12

10 The perception of emerging patterns as virtual retinal images

The last step of the models is to reconstruct, from planforms in $V1$, corresponding virtual retinal images.

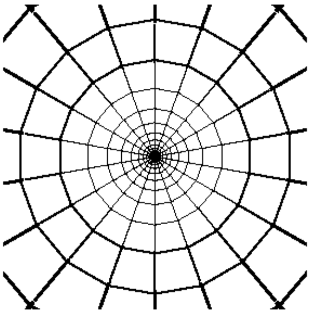
We consider thesimplest retinotopic conformal map $M : R \to V1$

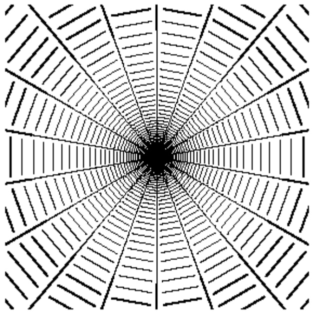
$$z_R = x_R + iy_R = \rho_R e^{i\theta_R} \mapsto z = x + iy = \log(z_R) = \log(\rho_R) + i\theta_R.$$

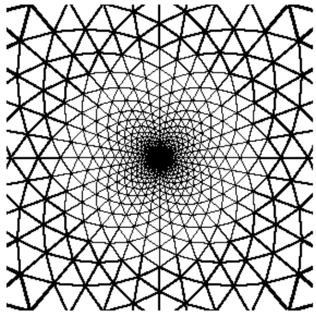
Lines in $V1$ correspond to spirals on the retina and, if φ_R is a local orientation on R at $\mathbf{x} = z = \rho_R e^{i\theta_R}$, it is projected by the tangent map to $\varphi = \varphi_R - \theta_R$.

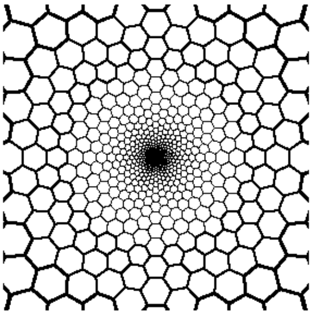
We apply the *inverse* M^{-1} of the conformal map to the planforms of the PDE and we get quite exact models of Klüver's planforms (see tables 13, 14, 15).

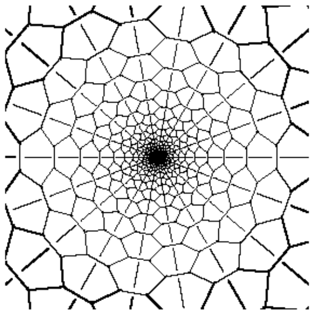
Klüver's planforms are isomorphic to eigenmodes of the bifurcated solution of the neural network in the synaptic weights of which the functional architecture of $V1$ *is encoded.*


1. Even squares.


2. Even rolls.


3. Even hexagons I.


4. Even hexagons II.


5. Even rhombs.

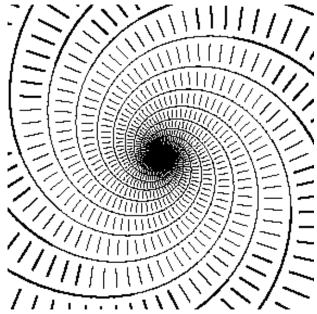
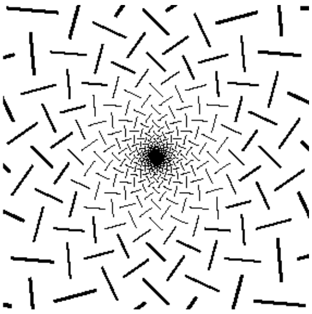
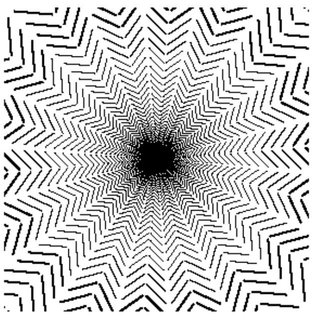
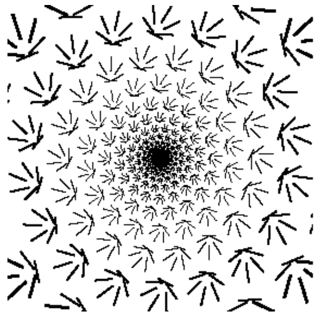
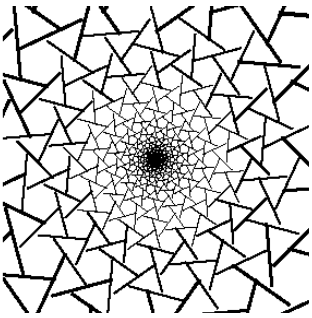

6. Even rhombic rolls.

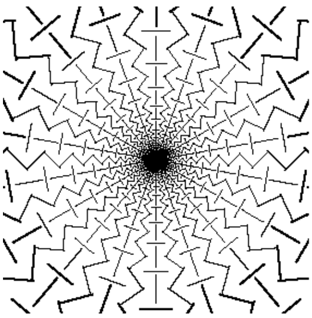
Table 13


1. Odd squares.


2. Odd rolls.


3. Odd hexagons I (triangles).


4. Odd hexagons II.


5. Odd rhombs.

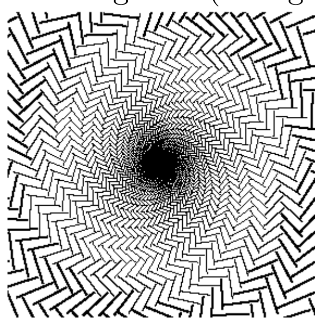
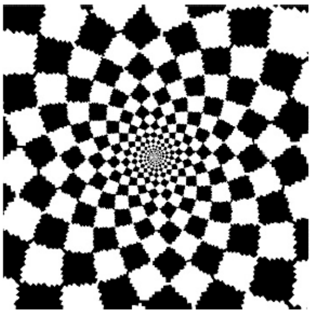
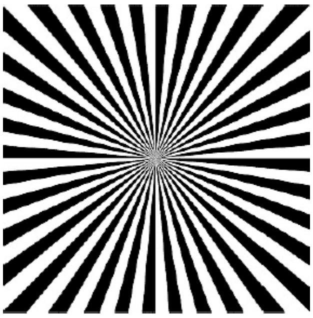

6. Odd rhombic rolls.

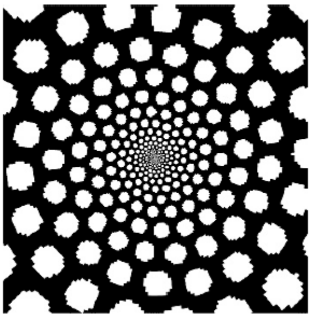
Table 14



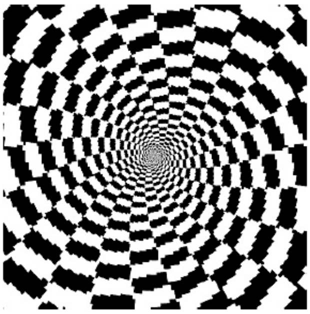
1. Non-contoured squares.



2. Non-contoured rolls.



3. Non-contoured hexagons.



4. Non-contoured rhombs.

Table 15

11 The problem of stability

A last (technical and difficult) issue is to study the *stability* of the solutions in order to select which of them can effectively appear in a bifurcation (see the paper).

12 Conclusion

Bressloff, Cowan, Golubitsky's papers show that many spontaneously emerging visual patterns can be explained as virtual retinal projections of spontaneous activations of $V1$. They provide a representation of its functional architecture.

It must be emphasized that they are not mere applications of already known models to computational neurosciences. Indeed, according to the authors, the bifurcation in the fibration $V1$ provide the first natural example of the pseudoscalar representation of $E(2)$.

Examples of improvements of these basic models:

1. Generalize the results beyond the hypothesis of minimal length critical wave vectors and beyond the application of the Equivariant Branching Lemma.

2. Take into account the fact that the fibration $\pi : R \times P \to R$ is naturally endowed with a *sub-Riemannian contact structure*.

3. Introduce other engrafted variables, and in particular a *scale* parameter. In the framework of contact geometry this correspond to the symplectization of the contact structure (joined work with Alessandro Sarti and Giovanna Citti).

4. Take into account other areas than $V1$.

5. Apply the techniques to cases where the input h doesn't vanish in the PDE (11).