MORPHOGENETIC "NEURON-FLOCKING":

DYNAMIC SELF-ORGANIZATION OF NEURAL ACTIVITY INTO MENTAL SHAPES

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grupo de estudios en biomimética



Morphogenetic "neuron flocking": The dynamic self-organization of neural activity into mental shapes

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Abstract – My aim is to contribute to a new research focus on the theoretical modeling of the "shapes" of multiscale spatiotemporal phenomena in large neural populations. I wish to emphasize the "complex systems" view of the brain as a recurrent network chiefly occupied with its own intrinsic, emergent activity (sometimes also called "ongoing activity", although this term is more evocative of a background nuisance than a core function). Traditionally, neural models have followed a rather naive paradigm of input/output signal processing, in which the system is considered passive and essentially stimulus-driven. We should now encourage a recent trend of computational neuroscience to move away from this linear reduction, in order to explore a dynamical paradigm of active self-organization. In this paradigm, stimuli only trigger or distort preexisting internal states, which have been molded and imprinted in synaptic connections during development and Hebbian-like learning. At one or several appropriate mesoscopic levels, the neocortex could be construed as a "pattern formation machine", generating specific dynamical regimes made of myriads of bioelectrical neuronal signals – not unlike many other biological collective phenomena such as bird flocking, ant colonies or, closer to neurons, multicellular development. Dynamical "neuron flocking", for its part, happens in phase space and across a complex network topology: What are the emergent mesoscopic objects of its dynamics? Can we characterize their fine spatiotemporal structure through experimental data and/or theoretical models? How are they are endogenously produced by the neuronal substrate - and exogenously evoked and perturbed by perceptual stimuli? How do they interact (bind and compose, breakup and compete) with each other and with motor action? I will present a few of my studies that have started to address these important questions of dynamical neural assembly and shape formation.



AND THE MORPHOGENETIC "NEURON-FLOCKING"





phase space view: complex spatiotemporal pattern = mental shape

(dynamic)

emergence? structure? properties?

(long-term) persistence? learning? storage? compositionality?

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physical space view: mega-MEA raster plot = activity of 10⁶-10⁸ neurons













Emergent Neurodynamics



MORPHOGENETIC "NEURON-FLOCKING"



1. Cognitive Architectures in the Tower of Complex Systems

The emergence of neural/mind states on multiple levels of self-organization

- From agents to collectives, via local interactions
 - From neurons to brain (anatomy)
 - From potentials to fMRI (physiology)
 - From connections to cognition (models)



Emergence on multiple levels of self-organization





From genotype to phenotype, via <u>development</u>





From pigment cells to coat patterns, via reaction-diffusion





From social insects to swarm intelligence, via stigmergy





From birds to flocks, via flocking





All agent types: molecules, cells, animals, humans & tech





From neurons to brain, via <u>neural development</u> (anatomy)







From potentials to fMRI, via synaptic transmission (physiology)

groups, societies

full brain imaging (fMRI) large fields (V-sensitive dyes) Population code (multielectrode) individual potential (electrode)

macromolecules





Raster plot of of a simulated synfire braid, Doursat et al. 2011







From connections to cognition, via <u>correlations</u> (modeling)



MORPHOGENETIC "NEURON-FLOCKING"



1. Cognitive Architectures in the Tower of Complex Systems The emergence of neural/mind states on multiple levels of self-organization

2. The Mind as a Pattern Formation Machine

Neural correlations: The glue of spatiotemporal patterns (STPs)

- The importance of temporal coding
- Pattern formation
- "Neuron flocking"
- Morphogenesis





> The importance of temporal coding

 \checkmark more than mean rates \rightarrow *temporal correlations* among spikes







Historical motivation for rate coding

- Adrian (1926): the firing rate of mechanoreceptor neurons in frog leg is proportional to the stretch applied
- Hubel & Wiesel (1959): selective response of visual cells; e.g., the firing rate is a function of edge orientation

 \rightarrow rate coding is confirmed in sensory system and primary cortical areas, however increasingly considered insufficient for <u>integrating</u> the information

Temporal coding pioneers of the 1980-90's

- von der Malsburg (1981): theoretical proposal to consider <u>correlations</u>
- Abeles (1982, 1991): precise, <u>reproducible spatiotemporal spike</u> <u>rhythms</u>, named "synfire chains"
- Gray & Singer (1989): stimulus-dependent <u>synchronization of</u> <u>oscillations</u> in monkey visual cortex
- O'Keefe & Recce (1993): <u>phase coding</u> in rat hippocampus supporting spatial location information
- Bialek & Rieke (1996, 1997): in H1 neuron of fly, <u>spike timing</u> conveys information about <u>time-dependent input</u>





The "binding problem": using temporal code









> More generallly: feature binding in cell assemblies

 unstructured lists or "sets" of features lead to the "superposition catastrophe"







"Grandmother" "Jennifer Aniston" cells... really?

 \bigcirc



 \bigcirc



 \bigcirc

₹**+** ₹



 \bigcirc





"blue-orange-red-3-book-stack" cell

→ one way to solve the confusion: introduce overarching hypercomplex detector cells













. . . however, this soon leads to a combinatorial explosion





> Instead: relational representation \rightarrow graph format

✓ a better way to solve the confusion: represent relational information with *graphs*







Idea: relational information can be encoded temporally

✓ back to the binding problem: a solution using temporal coding







➢ Beyond small graphs → large "spatiotemporal patterns"

- STPs: large-scale, localized dynamic cell assemblies that display complex, *reproducible* digital-analog regimes of neuronal activity
 - these regimes of activity are supported by specific, *ordered* patterns of recurrent synaptic connectivity





Scott Camazine, http://www.scottcamazine.com



Biological development is about pattern formation

✓ multicellular patterning















stripes Hubel & Wiesel, 1970 ocular dominance

"pinwheels" Blasdel, 1992 orientation column





Dynamics of orientation tuning: polar movie Sharon and Grinvald, Science 2002

... the brain is no different







In but beyond pattern formation: complex morphogenesis

✓ organisms are not just random, repetitive patterns but mostly complex, composite shapes endowed with a specific structure



"The stripes are easy, it's the horse part that troubles me" —attributed to A. Turing, after his 1952 paper on the chemical basis of morphogenesis





... but beyond pattern formation: complex morphogenesis

 STPs are not just random, repetitive patterns but mostly complex, composite shapes endowed with a specific structure







"Simple"/random vs. architectured complex systems







physical patterns

ina cell



organisms

il li diis

termite mounds



anima flocks

- a non-trivial, sophisticated morphology
 - *hierarchical* (multi-scale): regions, parts, details
 - modular: reuse of parts, quasi-repetition
 - heterogeneous: differentiation, division of labor
- ✓ random at agent level, reproducible at system level





Ex: Morphogenesis – Biological development







Nadine Peyriéras, Paul Bourgine et al. (Embryomics & BioEmergences)

cells build sophisticated organisms by division, genetic differentiation and biomechanical selfassembly

> Ex: Swarm intelligence – Termite mounds



Termite mound (J. McLaughlin, Penn State University)



http://cas.bellarmine.edu/tietjen/ TermiteMound%20CS.gif



Termite stigmergy (after Paul Grassé; from Solé and Goodwin, "Signs of Life", Perseus Books)

 termite colonies build sophisticated mounds by
"stigmergy" = loop between modifying the environment and reacting differently to these modifications



2. Morphogenetic Engineering

An Artificial Life agent model capturing the essence of morphogenesis





2. Morphogenetic Engineering

... and changing the agents' self-architecting behavior through evolution





2. Morphogenetic Engineering

... and changing the neurons' self-flocking behavior through learning?

A metaphor for a "mental shape zoo"? Neural morphogenesis extends beyond slow, 3-D physical development into fast, n-D spatio-temporal assemblies.

After cells have positioned themselves and established contacts, they continue "moving" and "assembling / disassembling" in virtual, phase space.



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Neural correlations: The glue of spatiotemporal patterns (STPs)

3. Example Model: Wave-Based Shape-Matching

Coding coordinates by phases, and shapes by waves

Lattices: group sync, waves, 2D shapes .

Synfire chains: wave storage, retrieval

Synfire braids: shape storage, matching





- Wave-based pattern retrieval and matching
 - ✓ Lattices of coupled oscillators (zero delays)
 - group synchronization
 - traveling waves
 - 2D wave shapes
 - shape metric deformation

✓ Synfire chains (uniform delays)

- wave propagation
- chain growth
- pattern storage and retrieval

✓ Synfire braids (transitive delays)

- shape storage and retrieval
- 2D wave-matching











- Lattice of coupled oscillators group sync, phase-tagging
 - the base of many perceptual segmentation models in the 1990's
 - <u>auditory</u>: von der Malsburg & Schneider (1986), "cocktail party" processor
 - visual, after Gray & Singer (1989): Kurrer & Schulten (1990), König & Schillen (1991), DL Wang & Terman (1995), Campbell & DL Wang (1996), etc.
 - oscillatory or excitable units as an abstraction of excit↔inhib columnar activity
 - **2D lattice coupling** as an abstraction of topographically organized visual cortex



(w/ relaxation oscillators similar to FitzHugh-Nagumo/Morris-Lecar + global inhibition)

Wang D.L. and Terman D. (1997): Image segmentation based on oscillatory correlation. Neural Computation, vol. 9, 805-836


3. Wave-Based Shape-Matching





input

term

$\blacktriangleright \text{ Lattice of coupled oscillators} \begin{cases} \frac{du_i}{dt} = c(u_i - \frac{u_i^3}{3} + v_i + z) + \eta + K_i + I_i \\ \frac{dv_i}{dt} = \frac{1}{c}(a - u_i - bv_i) + \eta \end{cases}$

- - proportional to the *u* signal difference only in spiking domain u < 00
 - positive connection weight k_{ii}
 - possible transmission delay τ_{ii}
 - here zero delays $\tau_{ii} = 0$ 0





coupling

term

 $K_{i}(t) = \sum_{\substack{j=1\\u_{j}(t-\tau_{ij})<0}}^{I} k_{ij} \left(u_{j}(t-\tau_{ij}) - u_{i}(t) \right)$











Wang D.L. and Terman D. (1997): Image segmentation based on oscillatory correlation. *Neural Computation*, vol. 9, 805-836





Lattice of coupled oscillators – traveling waves





Doursat,, R. & Petitot, J. (2005) Dynamical systems and cognitive linguistics: Toward an active morphodynamical semantics. *Neural Networks* **18**: 628-638.



- Lattice of coupled oscillators traveling waves
 - ✓ Random propagation
 - z = -0.346, k = 0.04, I = 0

✓ Circular wave generation

■ z = -0.29, k = 0.10, I = -0.44 (point stimulus •)





✓ Planar & mixed wave generation

• z = -0.29, k = 0.10, I = -0.44 (bar stimulus)









- > The "morphodynamic pond": a neural medium at criticality
 - \checkmark upon coupling onset and/or stimulation \rightarrow emergence of a wave
 - quick transition to ordered regime (STP): reproducible succession of spike events $(t^1, t^2, ...)$
 - ✓ the structure of the STP is a trade-off between
 - endogenous factors: connectivity (structural bias), attractors (preferred activation modes)
 exogenous factors: stimulus (perturbation), binding (composition with other STPs)



• 0 0 0









Lattice of coupled oscillators – 2D wave shapes

- coding coordinates with phases
- the salient "featuredetecting" units of an object can participate in 2 different STPs by propagation of 2 different waves
- similar to buoys floating on water



these 2 STPs form a 2D constellation or "shape" in virtual t_{x1}=t₀ phase space (timings)





Lattice of coupled oscillators – 2D wave shapes

- coding coordinates with phases
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- similar to buoys floating on water



 these 2 STPs form a 2D constellation or "shape" in virtual phase space (timings)











- Lattice of coupled oscillators 2D wave shapes
 - \checkmark the final shape in virtual phase space depends on
 - the physical position of the feature units on the lattice
 - the form and direction of the two waves, itself depending on:
 - o endogenous factors: connectivity and weight distribution
 - o exogenous factors: stimulus domains
 - ✓ ex: no deformation
 - planar & orthogonal waves
 - uniform weights on P_X and P_Y
 - o orthogonal full-bar stimuli
 - \rightarrow shape = physical positions





Px









- Lattice of coupled oscillators shape metric deformation
 - wave detection and velocity measure based on control units
 - the probability of wave generation increases with $z \searrow$ and $k \nearrow$
 - the velocity of the generated wave increases with $z \searrow$ and $k \nearrow$





Lattice of coupled oscillators – shape metric deformation

- ✓ ex: "shear stress" deformation
 - vertical wave + horizontal wave
 - o Y-gradient of weights on P_Y
 - o orthogonal full-bar stimuli













ex: "laminar flow" deformation

- Iaminar wave + vertical wave
 - *Y*-gradient of weights on P_X
 - o orthogonal full-bar stimuli





Lattice of coupled oscillators – shape metric deformation

0

10

20

Px

30

40

- ex: irregular deformation
 - heterogeneous waves

 - o orthogonal full-bar stimuli







D

10

20

30

40





Wave-based pattern retrieval and matching

- Lattices of coupled oscillators (zero delays)
 - group synchronization
 - traveling waves
 - 2D wave shapes
 - shape metric deformation

✓ Synfire chains (uniform delays)

- wave propagation
- chain growth
- pattern storage and retrieval

✓ Synfire braids (transitive delays)

- shape storage and retrieval
- 2D wave-matching











Synfire chains – definition

✓ a synfire chain (Abeles 1982) is a sequence of synchronous neuron groups $P_0 \rightarrow P_1 \rightarrow P_2$... linked by feedfoward connections that can support the propagation of waves of activity (action potentials)



- ✓ synfire chains have been hypothesized to explain neurophysiological recordings containing statistically significant delayed correlations
- ✓ the redundant divergent/convergent connectivity of synfire chains can preserve accurately synchronized action potentials, even under noise





Synfire chains – *typical example studies*

✓ 1-chain propagation viability

mental shape = stability

Diesmann, Gewaltig & Aertsen (1999) Stable propagation of synchronous spiking in cortical neural networks

✓ 1-chain self-organized growth

mental shape *learning* Doursat & Bienenstock (1991, 2006) *Neocortical selfstructuration as a basis for learning*

✓ 2-chain binding (\rightarrow see Section 4.)

mental shape
composition

memory

Abeles, Hayon & Lehmann (2004) *Modeling Compo*sitionality by Dynamic Binding of Synfire Chains

N-chain storage capacity

- mental shape Bienenstock (1995) A model of neocortex
 - Trengove (2007) Storage capacity of a superposition of synfire chains using conductance-based I&F neurons







Chain 1



synfire chains potential fill all the requirements for a mesoscopic world of mental shapes



Synfire chains – self-organized growth



Doursat, R. (1991), Doursat & Bienenstock, E. (2006) Neocortical self-structuration as a basis for learning. *5th International Conference on Development and Learning (ICDL 2006)*, May 31-June 3, 2006, Indiana University, Bloomington, IN. IU, ISBN 0-9786456-0-X.





Synfire chains – self-organized growth

a special group of n_0 synchronous cells, P_0 , is repeatedly (not necessarily periodically) activated and recruits neurons "downstream"

if *i* fires once after P_{0} , its weights increase and give it a 12% chance of doing so again (vs. 1.8% for the others)





- Synfire chains pattern mix and selective retrieval
 - \checkmark random renumbering and uniform rewiring (column \rightarrow column probability p)





Synfire chains – *pattern mix and selective retrieval*

✓ statistics of selective retrieval depending on input size (in first pool)







Wave-based pattern retrieval and matching

- Lattices of coupled oscillators (zero delays)
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✓ Synfire chains (uniform delays)

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- pattern storage and retrieval

Synfire braids (transitive delays)

- shape storage and retrieval
- 2D wave-matching









Synfire braids – *definition*

- ✓ synfire braids (Bienenstock 1991, 1995) are generalized STPs with longer delays among nonconsecutive neurons, without distinct synchronous groups
- ✓ they were rediscovered later as "polychronous groups" (Izhikevich 2006)





Izhikevich 2006

- ✓ in a synfire braid, delay transitivity $\tau_{AB} + \tau_{BC} = \tau_{AD} + \tau_{DC}$ supports incoming spike coincidences, hence stable propagation of activity
- ✓ synfire braids can also grow in a network with nonuniform integer-valued delays τ_{ij} and inhibitory neurons



weights B





same layout, same shape, different wiring (wrap-around)

✓ high stimulus specificity

to generate a wave, a synfire braid needs a minimum of *N* neurons stimulated in a sequence ("sub-STP") compatible with the delays

mixed weights A + weights B







 $\tau = 15$

= 10

simultaneously \rightarrow no wave

weights A



- Synfire braids pattern mix and selective retrieval
 - statistics of selective retrieval depending on input size (in sequence)



 \checkmark statistics of selective retrieval depending on input size and p or τ







Synfire braids – shape mix and selective retrieval

same layout, different shape



to generate a wave, a synfire braid needs a minimum of N neurons stimulated in a sequence ("sub-STP") compatible with the delays





simultaneously \rightarrow no wave





Synfire braids – *wave-matching*

 ✓ graph-matching implemented as dynamical link matching between two pairs of STPs

$$\frac{du_i}{dt} = c(u_i - \frac{u_i^3}{3} + v_i + z) + \eta + K_i$$
$$\frac{dv_i}{dt} = \frac{1}{c}(a - u_i - bv_i) + \eta$$





Synfire braids – *wave-matching*

- additional coupling term: $W_i^{Xx}(t) = \sum_{\substack{j=1\\u_{i'}^x(t)<0}}^N w_{ii'}(t) \left(u_{i'}^x(t) u_i^X(t) \right)$
- ✓ where $w_{ii'}$ varies according to
 - 1. Hebbian-type synaptic plasticity based on temporal correlations

$$\Delta w_{ii'}(t) = \alpha \Big(-w_{ii'}(t) + w_0 f(s_{ii'}^{Xx}(0)) \Big) \quad \text{with}$$
$$s_{ii'}^{Xx}(0) = \langle u_i^X(t') \ u_{i'}^x(t') \rangle_{t=T}^t \quad \text{and} \quad f(s) = (1 + e^{-\lambda(s-s_0)})^{-1}$$

2. competition: renormalize efferent links

$$w_{ii'} \rightarrow w_{ii'} / \sum_j w_{ji'}$$

3. label-matching constraint





Synfire braids – 2D wave-matching

 $\textbf{Hebbian rule in 2D:} \quad \Delta w_{ii'}(t) = \alpha \Big(-w_{ii'}(t) + w_0 f \Big(\sqrt{s_{ii'}^{Xx}(0) s_{ii'}^{Yy}(0)} \Big) \Big) \\ s_{ii'}^{Xx}(0) = \langle u_i^X(t') \ u_{i'}^x(t') \rangle_{t-T_s}^t \quad f(s) = (1 + e^{-\lambda(s-s_0)})^{-1}$









Synfire braids – 2D wave-matching

- \checkmark to drive the system to the best match (global minimum), internal coupling k in graph-2 layer is regularly lowered and increased again
 - if match is weak, this will perturb STP 2 and undo matching links
 - if match is strong, this will not perturb STP 2 because it will be sustained by matching links → *resonance* between links and STPs

global "correlation" order parameter S:

$$S(t) = \frac{1}{N(N-1)} \sum_{i \neq j} \langle u_i(t') \ u_j(t'-\tau_{ij}) \rangle_{t-T_s}^t$$



weak (mis)match \rightarrow undone by uncoupling

global "synchronicity" order parameter *C*:

$$C(t) = \frac{1}{N(N-1)} \sum_{i \neq j} \cos\left(\frac{2\pi}{T} (t_i(t) - t_j(t) - \tau_{ij})\right)$$



strong match \rightarrow resistant to uncoupling

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Neural correlations: The glue of spatiotemporal patterns (STPs)

3. Example Model: Wave-Based Shape-Matching

Coding coordinates by phases, and shapes by waves

4. Shape-Based Compositionality STPs: The building blocks of mental shapes













(a) John gives a book to Mary.
(b) Mary gives a book to John.
(c)* Book John Mary give.





✓ language as a construction game of "building blocks"





✓ language as a construction game of "building blocks"







✓ language as a construction game of "building blocks"







- language, perception,
 cognition are a game of
 building blocks
- mental representations are internally *structured*
- elementary components
 assemble dynamically
 via temporal binding



Ex: synfire patterns can bind, i.e. support compositionality

 cognitive compositions could be analogous to conformational interactions among proteins...

after Bienenstock (1995) and Doursat (1991)

in which the basic "peptidic" elements could be *synfire chain* or *braid* structures supporting traveling waves

> two synfires can bind by synchronization through *coupling links*



hemoglobin

→ molecular metaphor


Sync & coalescence in a "self-woven tapestry" of chains

 multiple chains can "crystallize" from intrinsic "inhomogeneities" in the form of "seed" groups of synchronized neurons



see Bienenstock (1995), Abeles, Hayon & Lehmann (2004), Trengrove (2005)

- concurrent chain development defines a *mesoscopic scale of neural organization*, at a finer granularity than macroscopic AI symbols but higher complexity than microscopic neural potentials
- ✓ on this substrate, the dynamical binding & coalescence of multiple synfire waves provides the basis for compositionality and learning

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5. Toward Emergent Neurodynamics

Leaving "signal processing" for dynamic self-assembly





> The naive engineering paradigm: "signal processing"

- *feed-forward* structure activity literally "moves" from one corner to another, from the input (problem) to the output (solution)
- *activation* paradigm neural layers are initially silent and are literally "activated" by potentials transmitted from external stimuli
- *coarse-grain* scale a few units in a few layers are already capable of performing complex "functions"







It is not because the brain is an intricate network of microscopic causal transmissions (neurons activating or inhibiting other neurons) that the appropriate description at the mesoscopic functional level should be "signal / information processing".

This denotes a confusion of levels: mesoscopic dynamics is <u>emergent</u>, i.e., it creates mesoscopic objects that obey mesoscopic laws of interaction and assembly, qualitatively different from microscopic signal transmission





> The emergent dynamical paradigm: excitable media

- recurrent structure activity can "flow" everywhere on a fast time scale, continuously forming new patterns; output is in the patterns
- *perturbation* paradigm dynamical assemblies are already active and only "influenced" by external stimuli and by each other
- *fine-grain* Scale myriads of neurons form quasi-continuous media supporting structured pattern formation at multiple scales







- Tenet 1: mesoscopic neural pattern formation is of a fine spatiotemporal nature
- Tenet 2: mesoscopic STPs are individuated entities that are
 - a) endogenously produced by the neuronal substrate,
 - b) exogenously evoked & perturbed under the influence of stimuli,
 - c) interactively binding to each other in competitive or cooperative ways.





a) Mesoscopic patterns are endogenously produced

- ✓ given a certain connectivity pattern, cell assemblies exhibit various possible *dynamical regimes*, modes, patterns of ongoing activity
- the underlying connectivity is itself the product of *epigenetic* development and *Hebbian* learning, from activity



→ the identity, specificity or stimulus-selectiveness of a mesoscopic entity is largely determined by its internal pattern of connections





b) Mesoscopic patterns are exogenously influenced

- external stimuli (via other patterns) may *evoke & influence* the pre-existing dynamical patterns of a mesoscopic assembly
- it is an indirect, *perturbation* mechanism; not a direct, activation mechanism



 mesoscopic entities may have stimulus-specific *recognition or "representation"* abilities, without being "templates" or "attractors" (no resemblance to stimulus)





c) Mesoscopic patterns interact with each other

- populations of mesoscopic entities can *compete & differentiate* from each other to create specialized recognition units
- and/or they can *bind* to each other to create composed objects, via some form of temporal coherency (sync, fast plasticity, etc.)



evolutionary population paradigm molecular compositionality paradigm

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