

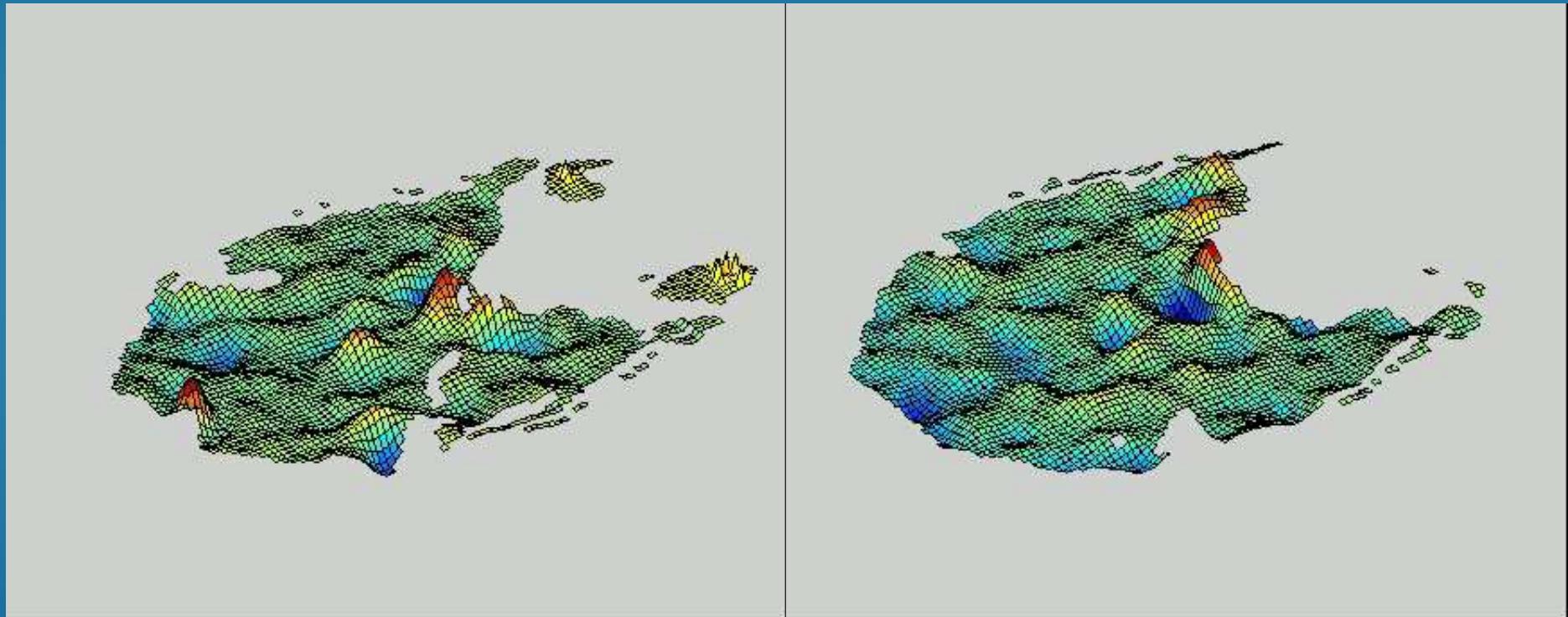


The Brain Dynamics Centre www.brain-dynamics.net

Westmead Hospital & University of Sydney



Modelling neural dynamics within a multiscale architecture



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“The best model of a cat is a cat
- preferably the same cat”

I: Dynamics

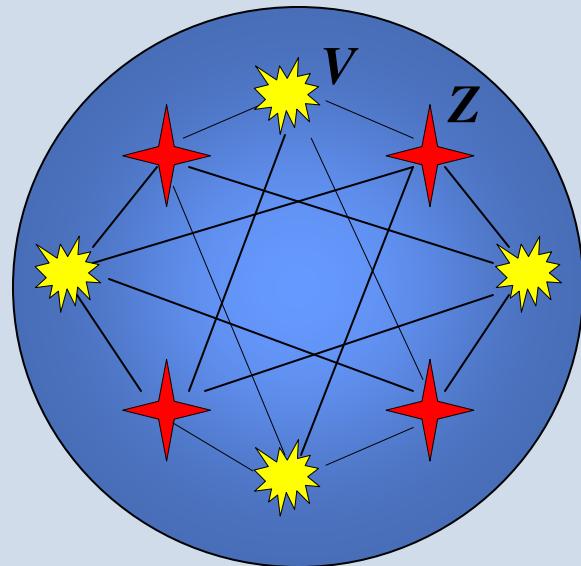


We adopt an approach which views the whole brain as governed by deterministic dynamical processes

1. The Basic Model: Pyramidal Cells

We begin by modelling a local ensemble of interconnected Pyramidal cells (V) and Inhibitory cells (Z).

Potassium channels (W) are also modelled dynamically



1. The Basic Model: Pyramidal Cells

$$C \frac{dV}{dt} = -g_{Ca}m_{Ca}(V - V_{Ca}) - g_{na}m_{na}(V - V_{na}) - g_KW(V - V_K) - g_L(V - V_L),$$

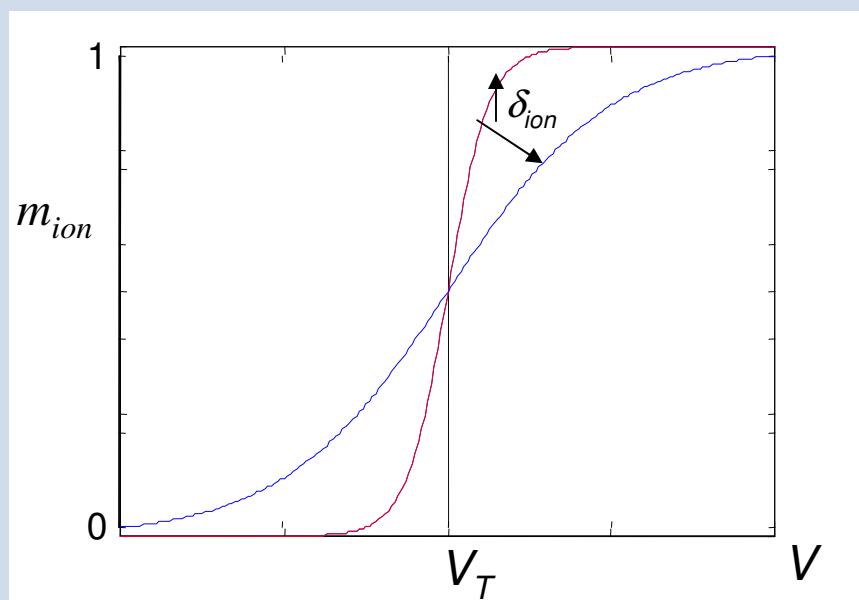
Maximum conductance of each ion species

Nernst potential of each ion species

Proportion of open voltage-gated ion channels

$$m_{ion} = 0.5 \left(1 + \tanh \left(\frac{V - V_T}{\delta_{ion}} \right) \right),$$

Nonlinear neural ‘activation function’ (Freeman 1975,79)
– also Haken, Lopez da Silva

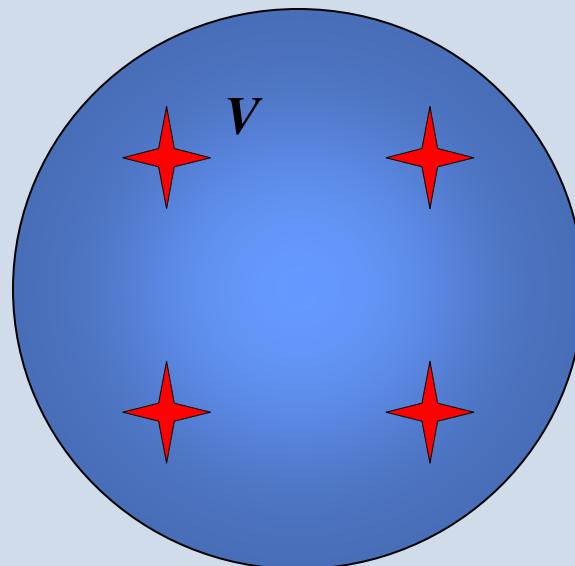


1. The Basic Model: Potassium Channels

$$\frac{dV}{dt} = -\sum g_{ion} m_{ion} (V - V_{ion}) + I_\delta,$$

$$\frac{dW}{dt} = \phi \frac{(m_k - W)}{\tau},$$

This permits an exponential relaxation of K⁺ channels between their open and closed conformations (other ion channels change directly with membrane potential)



1. The Basic Model: Inhibitory Cells

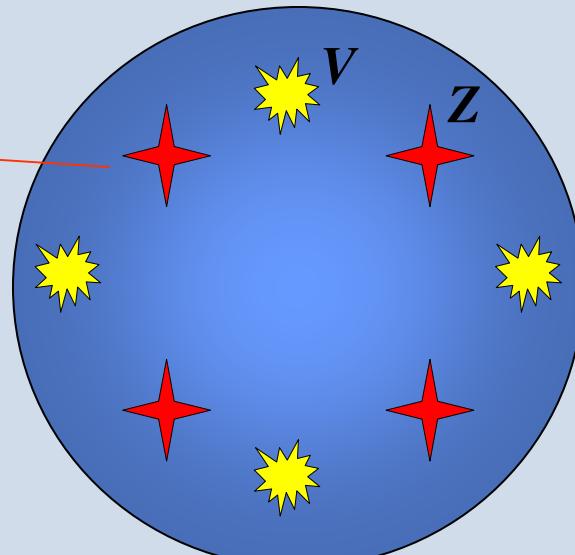
$$\frac{dV}{dt} = -\sum g_{ion} m_{ion} (V - V_{ion}) + I_\delta,$$

$$\frac{dW}{dt} = \phi \frac{(m_k - W)}{\tau},$$

$$\frac{dZ}{dt} = b(a_{ni} I).$$

$$Q_V = 0.5xQ_{V_{\max}} \left(1 + \tanh \left(\frac{V - V_T}{\delta_V} \right) \right),$$

$$Q_Z = 0.5xQ_{Z_{\max}} \left(1 + \tanh \left(\frac{Z - Z_T}{\delta_Z} \right) \right).$$



Larter *et al.* (1999) *Chaos*.

1. The Basic Model: Local Subsystem

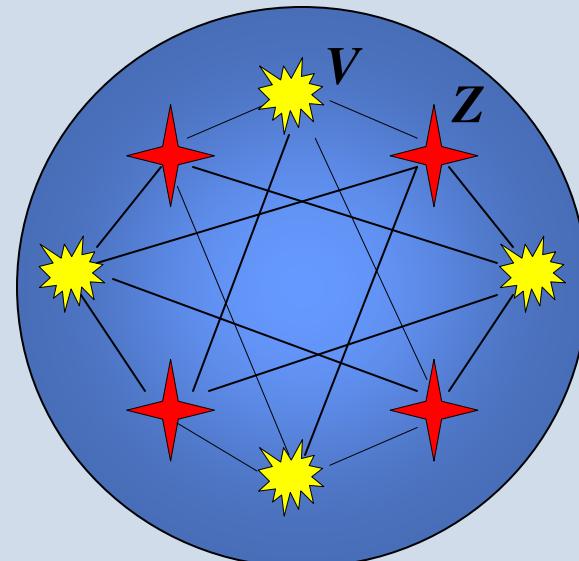
$$\frac{dV}{dt} = -\sum g_{ion} m_{ion} (V - V_{ion}) + I_\delta + a_{ie} Z \cdot Q_Z$$

$$\frac{dW}{dt} = \phi \frac{(m_k - W)}{\tau},$$

$$\frac{dZ}{dt} = b(a_{ni}I + a_{ei}V \cdot Q_V),$$

$$Q_V = 0.5xQ_{V_{max}} \left(1 + \tanh \left(\frac{V - V_T}{\delta_V} \right) \right),$$

$$Q_Z = 0.5xQ_{Z_{max}} \left(1 + \tanh \left(\frac{Z - Z_T}{\delta_Z} \right) \right).$$



Larter *et al.* (1999) *Chaos*.

1. The Basic Model: Local Subsystem

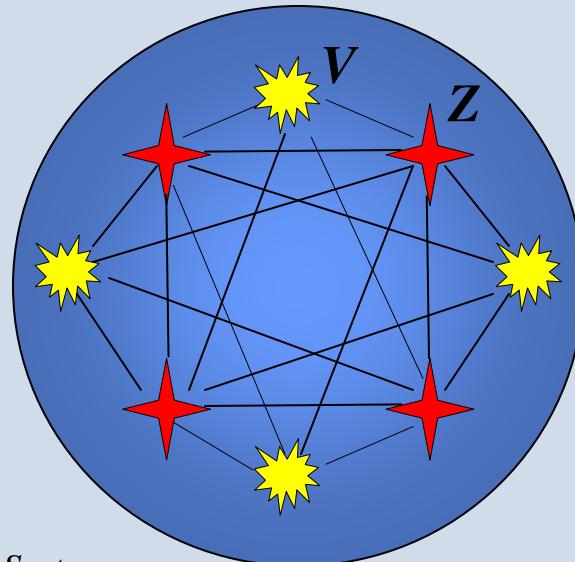
$$\frac{dV}{dt} = -\sum g_{ion} m_{ion} (V - V_{ion}) + I_\delta + a_{ie} Z \cdot Q_Z + \frac{g_{glut} a_{ee} Q_V (V - V_{na})}{},$$

$$\frac{dW}{dt} = \phi \frac{(m_k - W)}{\tau},$$

$$\frac{dZ}{dt} = b(a_{ni} I + a_{ei} V \cdot Q_V),$$

$$Q_V = 0.5xQ_{V_{max}} \left(1 + \tanh \left(\frac{V - V_T}{\delta_V} \right) \right),$$

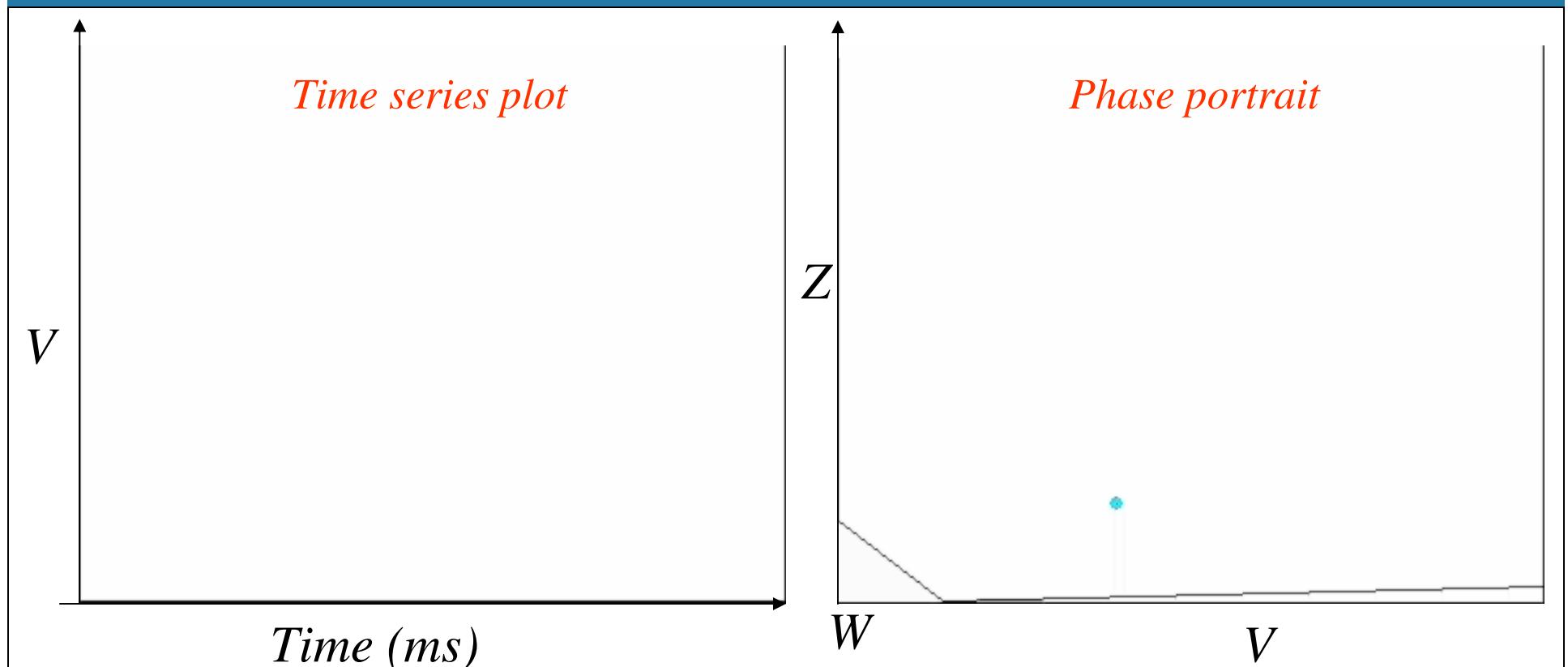
$$Q_Z = 0.5xQ_{Z_{max}} \left(1 + \tanh \left(\frac{Z - Z_T}{\delta_Z} \right) \right).$$



Breakspear, Terry, Friston. (2004) *Network: Computation in Neural Systems*

1. The Basic Model: Local Subsystem Dynamics

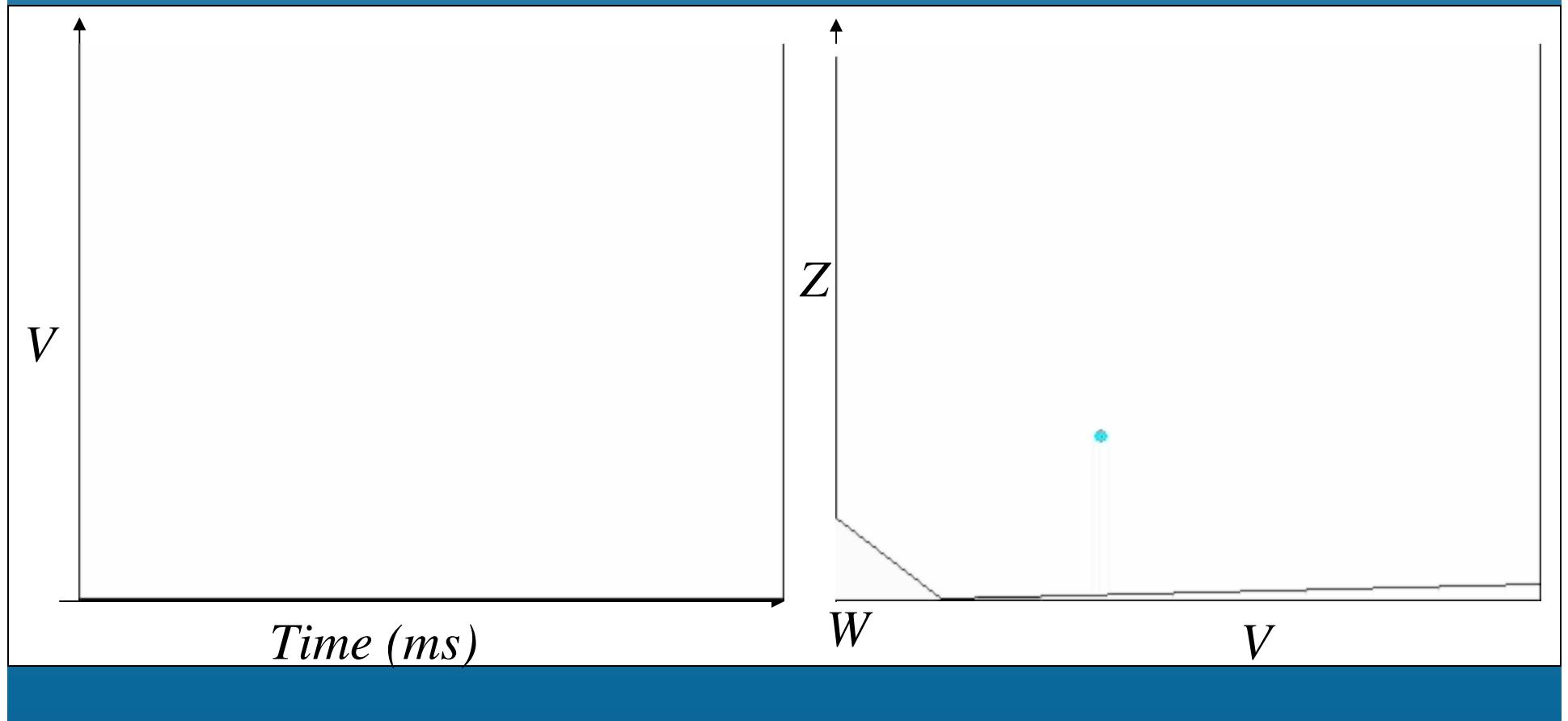
- Parameters approximate physiological range
- Random initial conditions
- One ‘control’ parameter – such as V_T



Steady state:

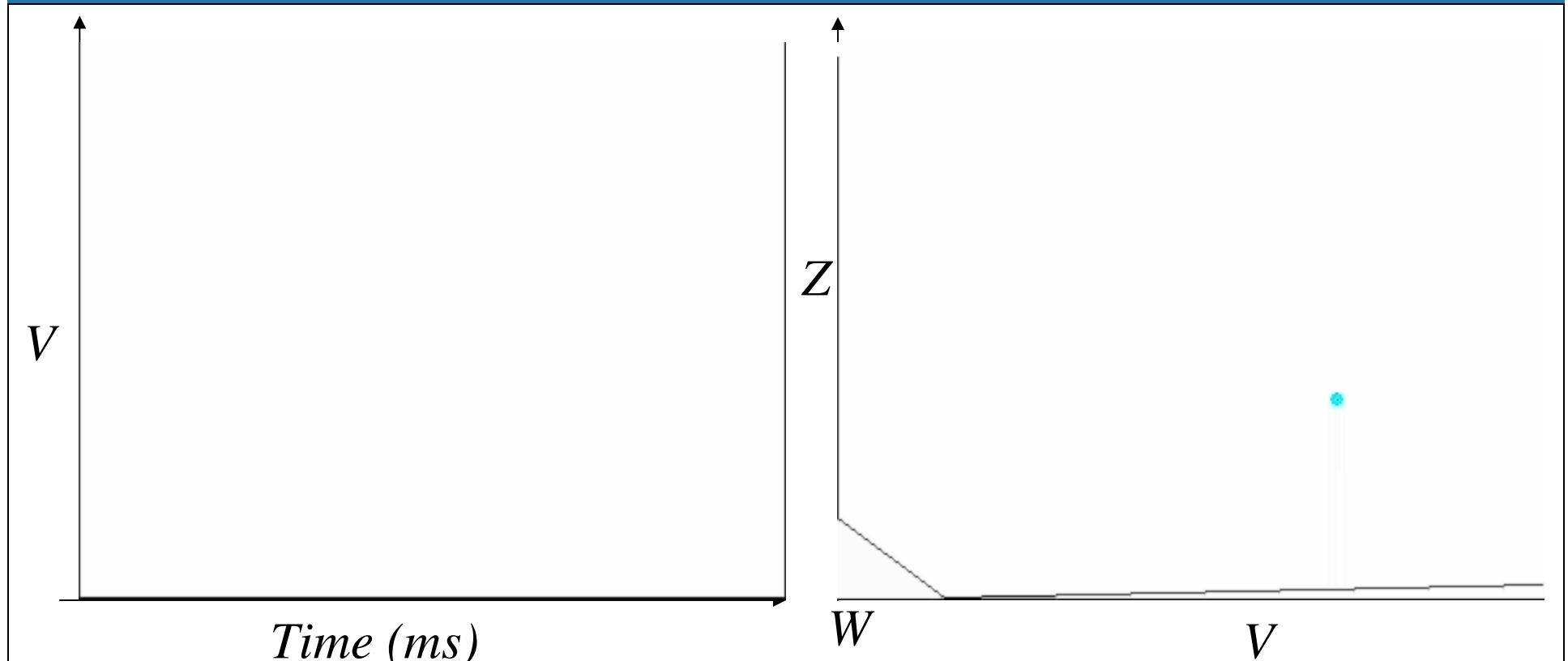
1. The Basic Model: Local Subsystem Dynamics

Simple and complex periodic behaviors



1. The Basic Model: Local Subsystem Dynamics

Aperiodic (chaotic) oscillations



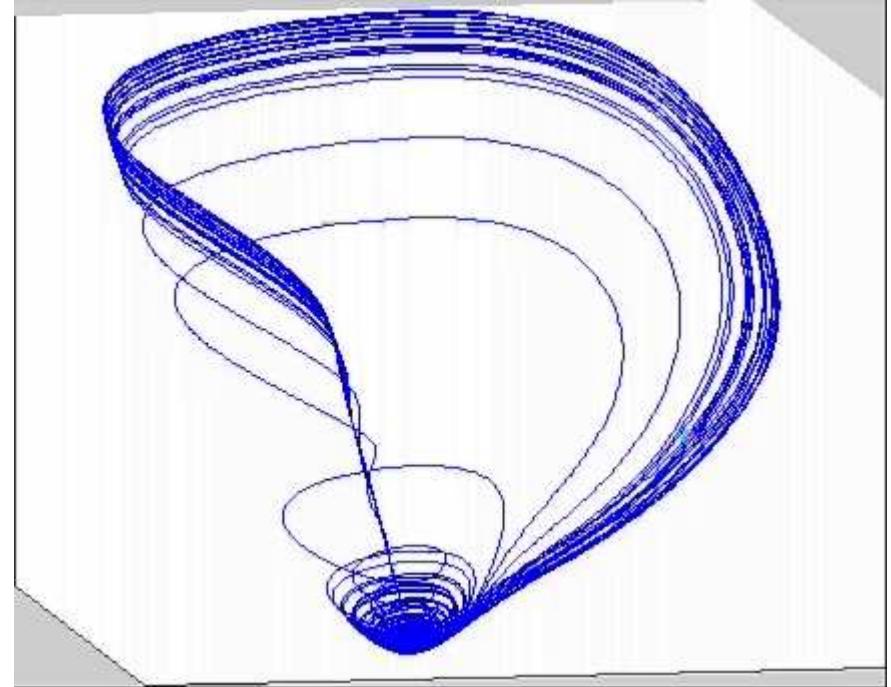
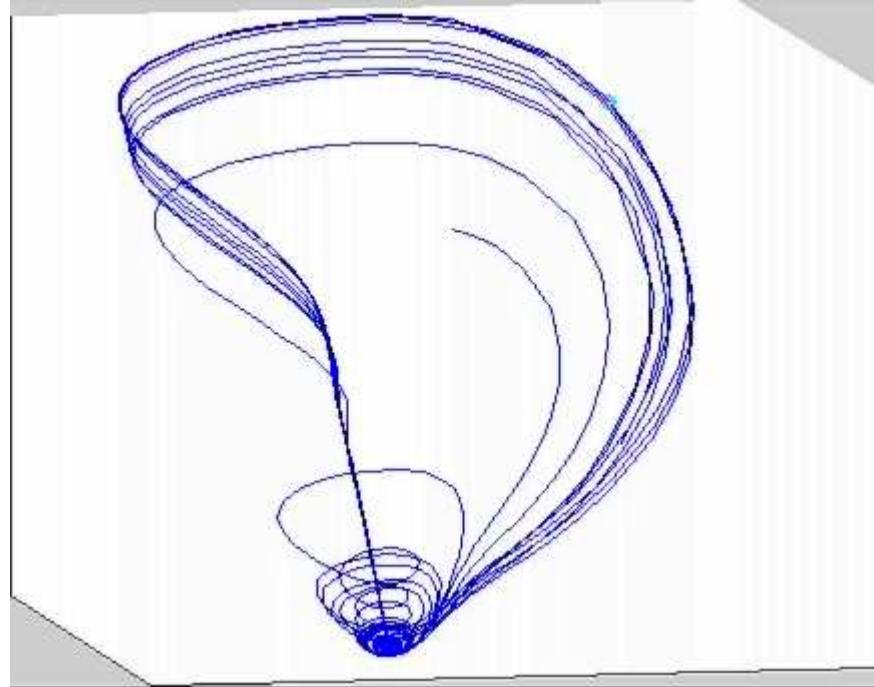
1. The Basic Model: Local Subsystem Dynamics

Homoclinic chaos: Lyapunov spectra =

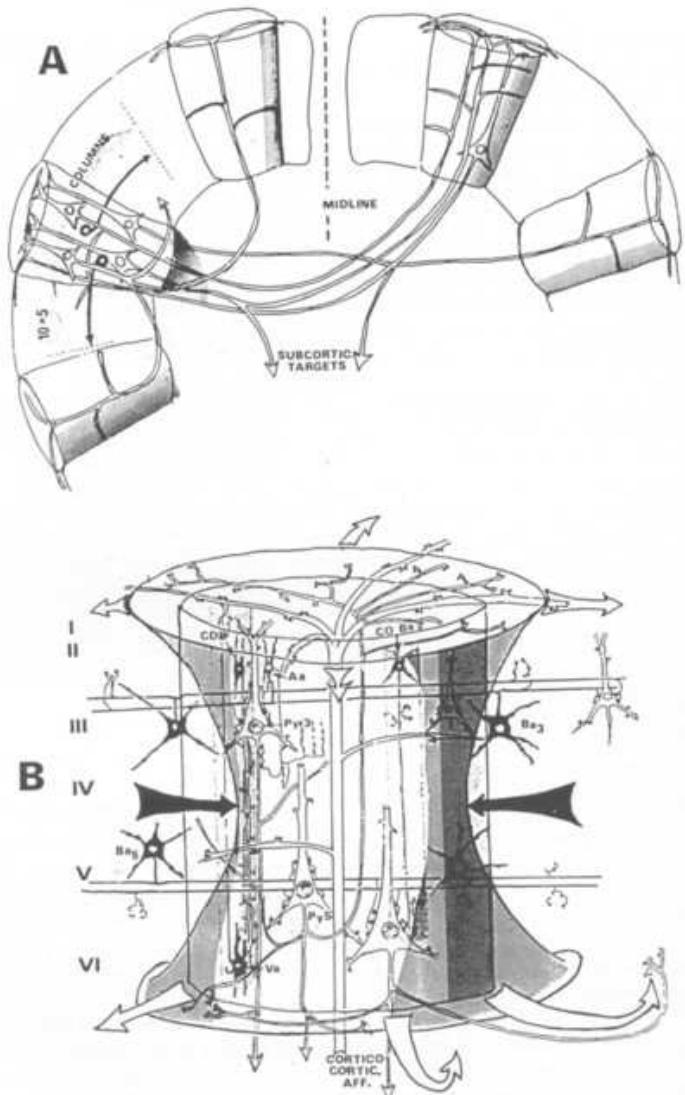
$$\Lambda_1 = 0.015,$$

$$\Lambda_2 = 0.0,$$

$$\Lambda_3 = -0.26.$$



1. The Basic Model: Coupled Subsystems



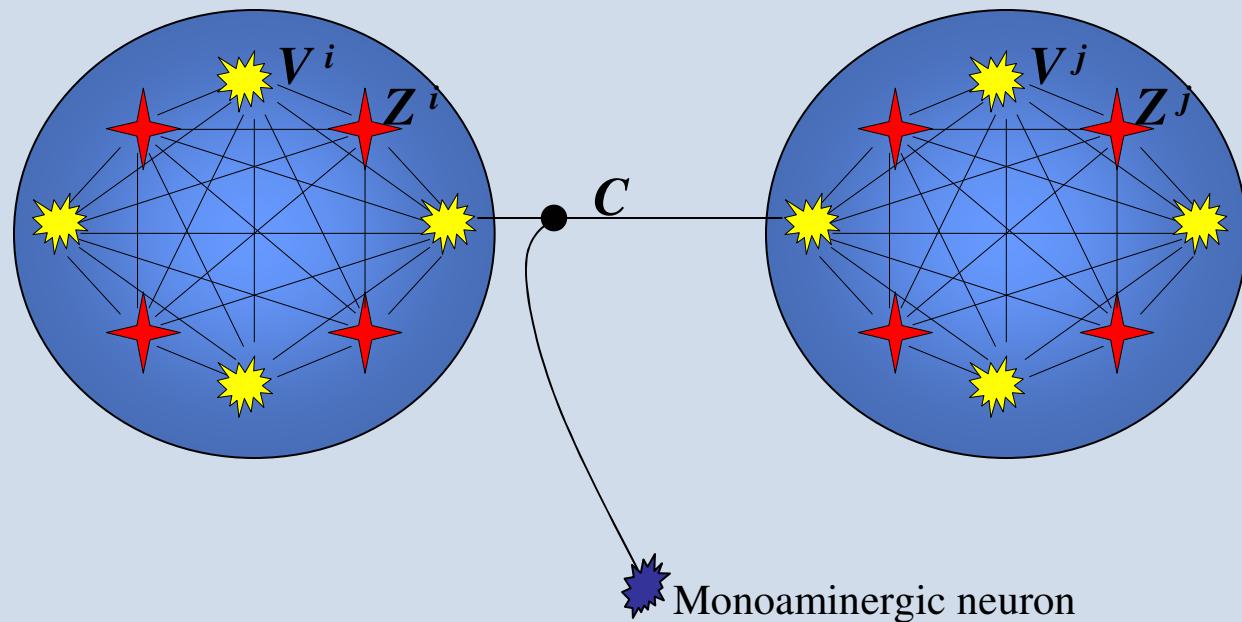
Nunez, PL (1995) *Neocortical Dynamics and Human Brain Rhythms*, Oxford University Press: Oxford.

The modular organization of the neuropil is a key feature of neural organization.

Modularity is evident across a hierarchy of scales – neurons, minicolumns, cortical columns, cortical regions, etc

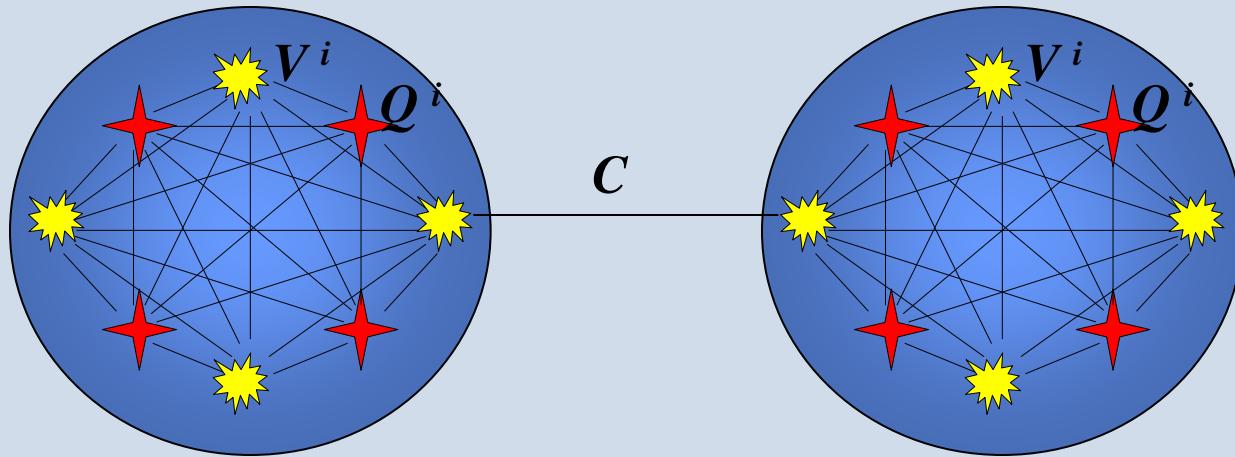
1. The Basic Model: Coupled Subsystems

- A cortical-like neural system is constructed by competitive excitatory-to-excitatory synaptic coupling



The strength of this excitatory coupling is modulated by a parameter that models ascending monoaminergic neurons

1. The Basic Model: Coupled Subsystems

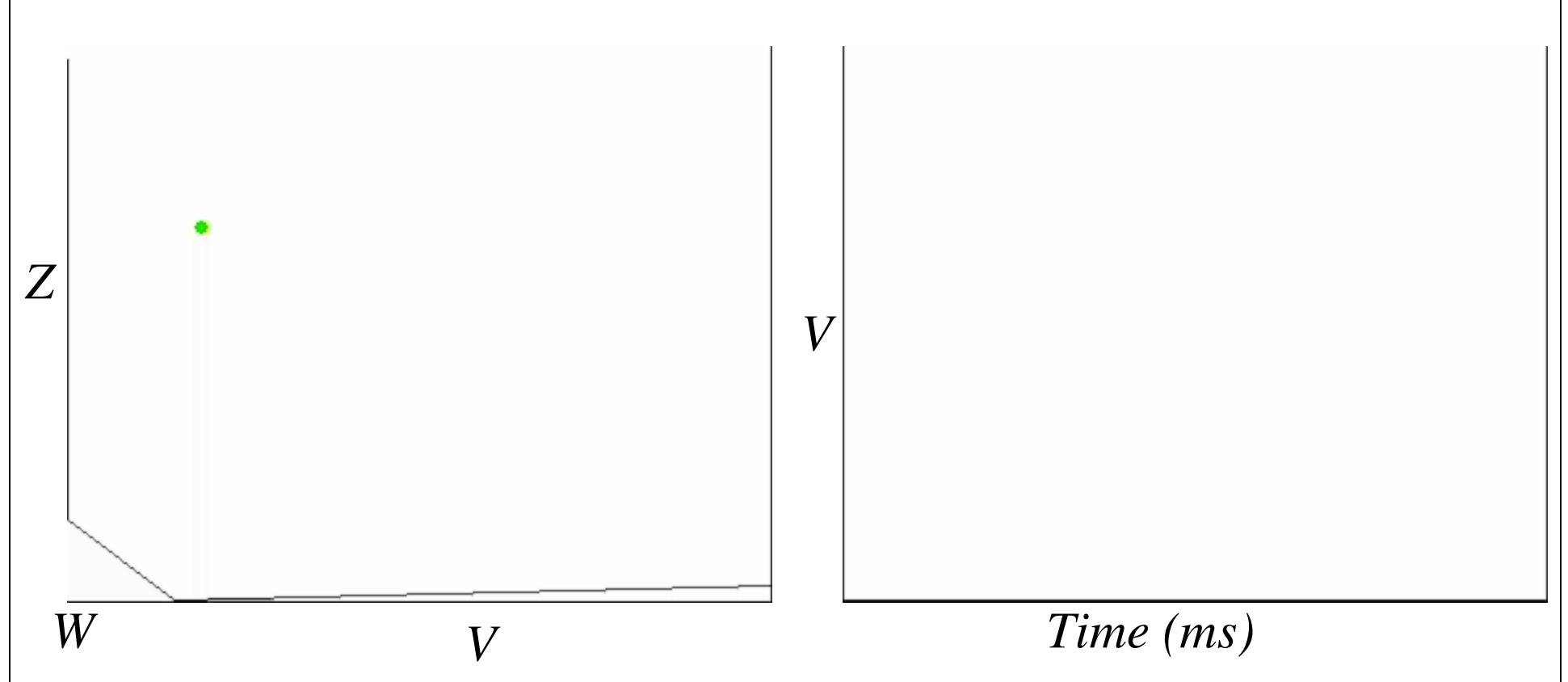


This is achieved by modifying the evolution of the local pyramidal cells to,

$$\frac{dV^i}{dt} = f(V^i, Q_V^i, Z^i, W^i) + g_{glut} a_{ee} (V - V_{na}) (C \cdot Q_V^j + (1 - C) Q_V^i),$$

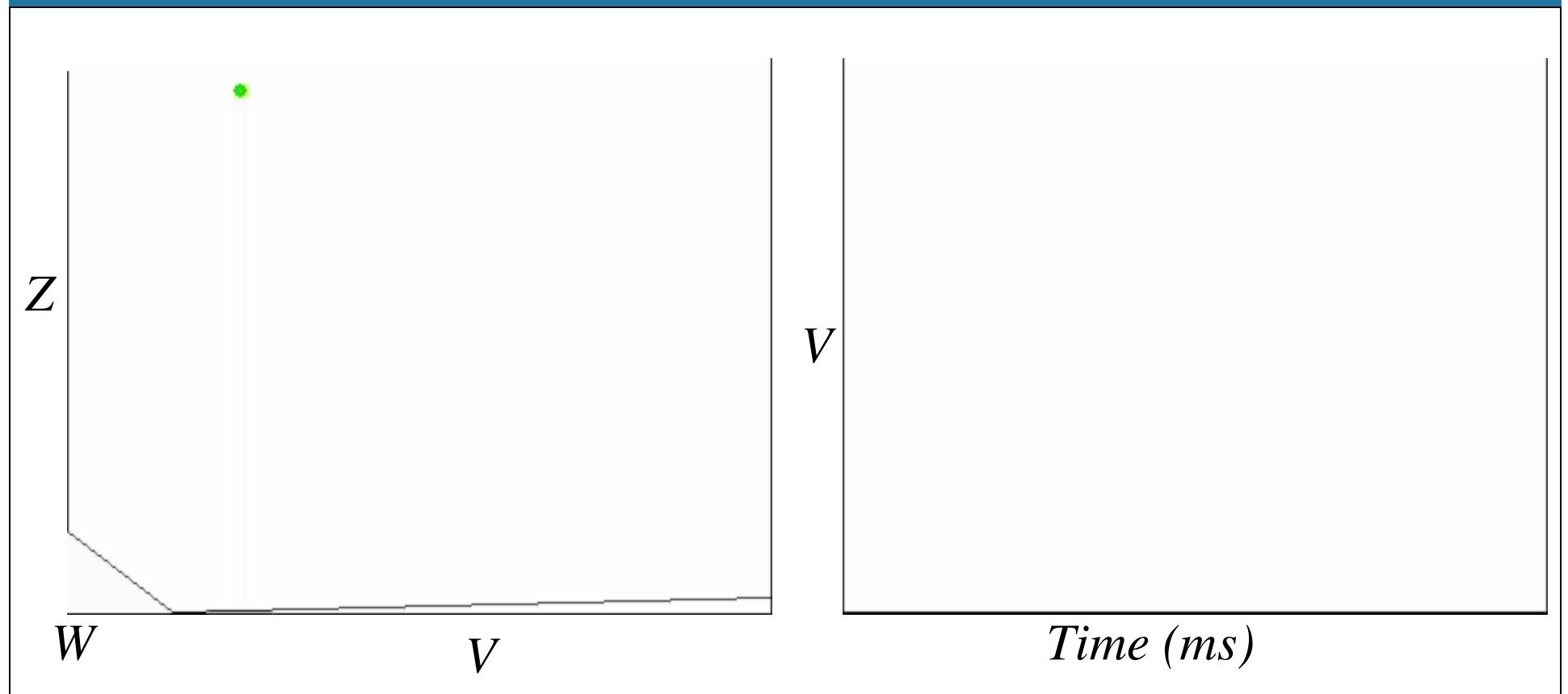
2. Nonlinear interdependence: No coupling

Without coupling ($C=0$), the systems evolve independently;



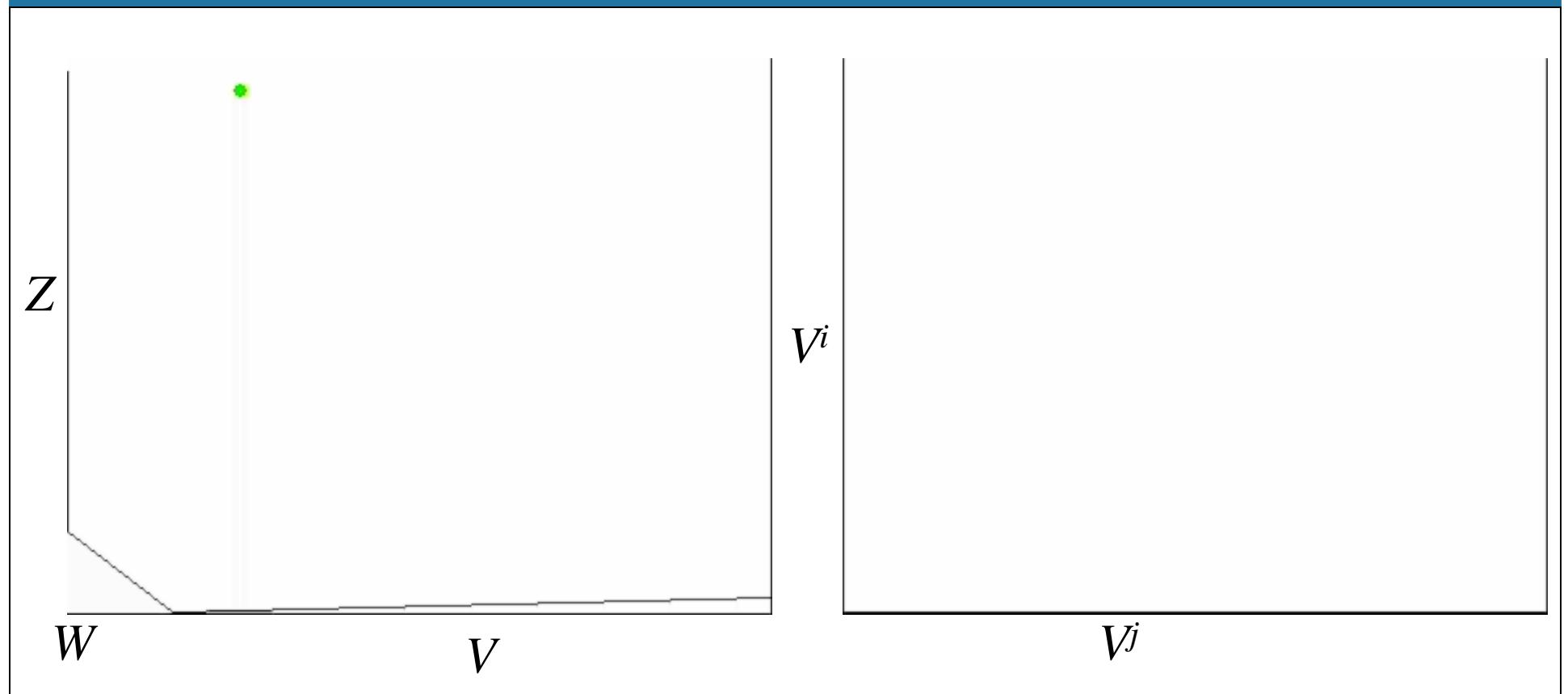
2. Nonlinear interdependence: Strong coupling

With $C=0.2$, there is a rapid approach to ***identical synchronization*** ($V^i = V^j$)



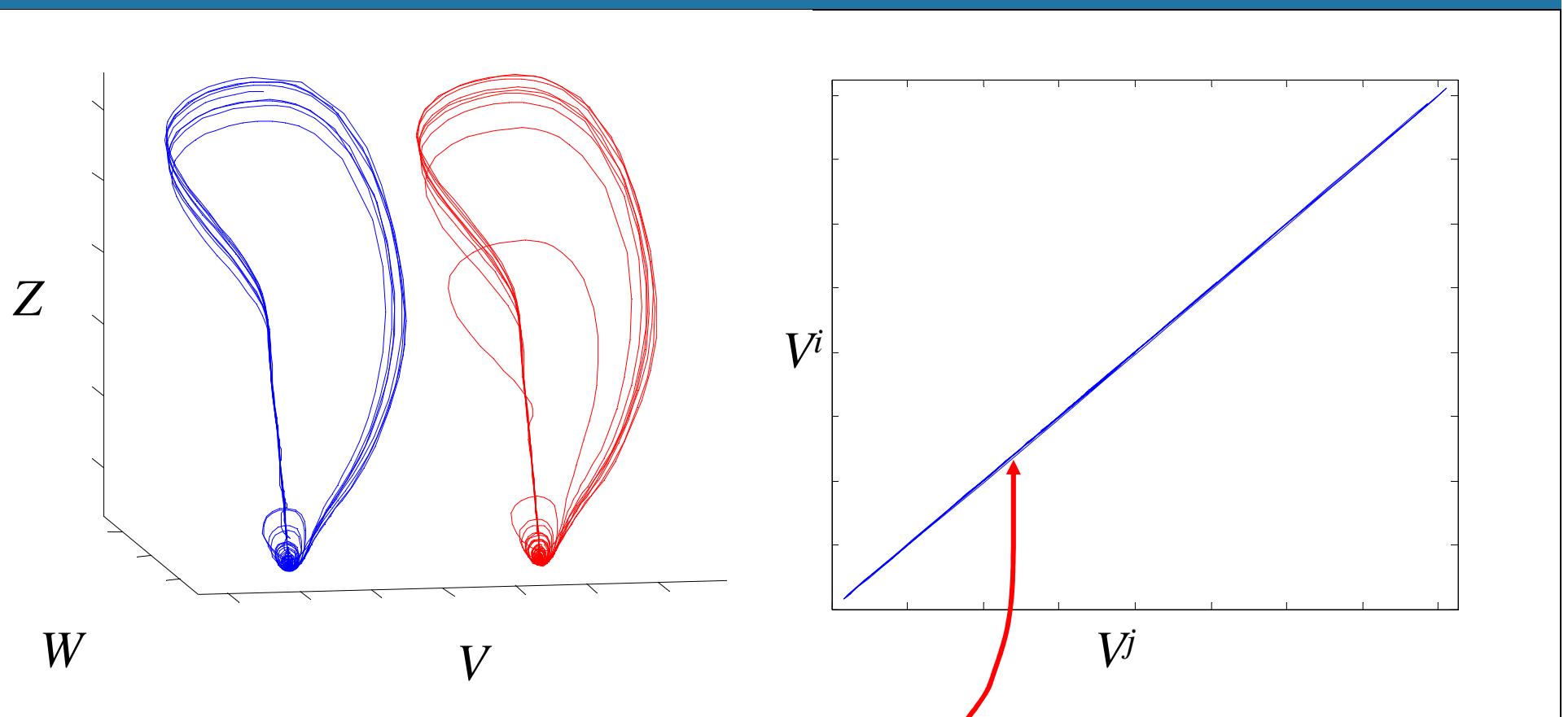
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2. Nonlinear interdependence: Strong coupling

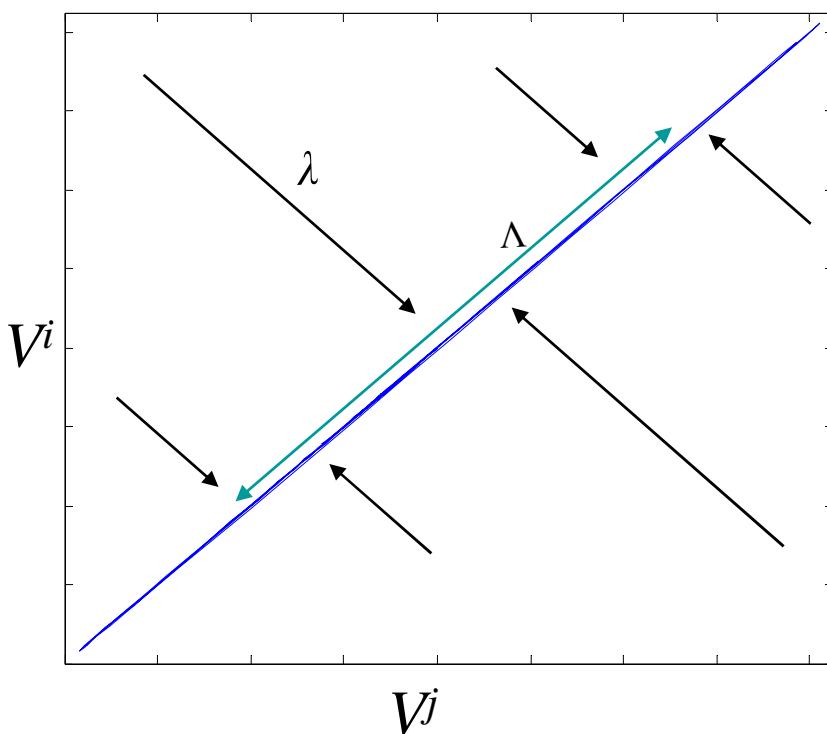
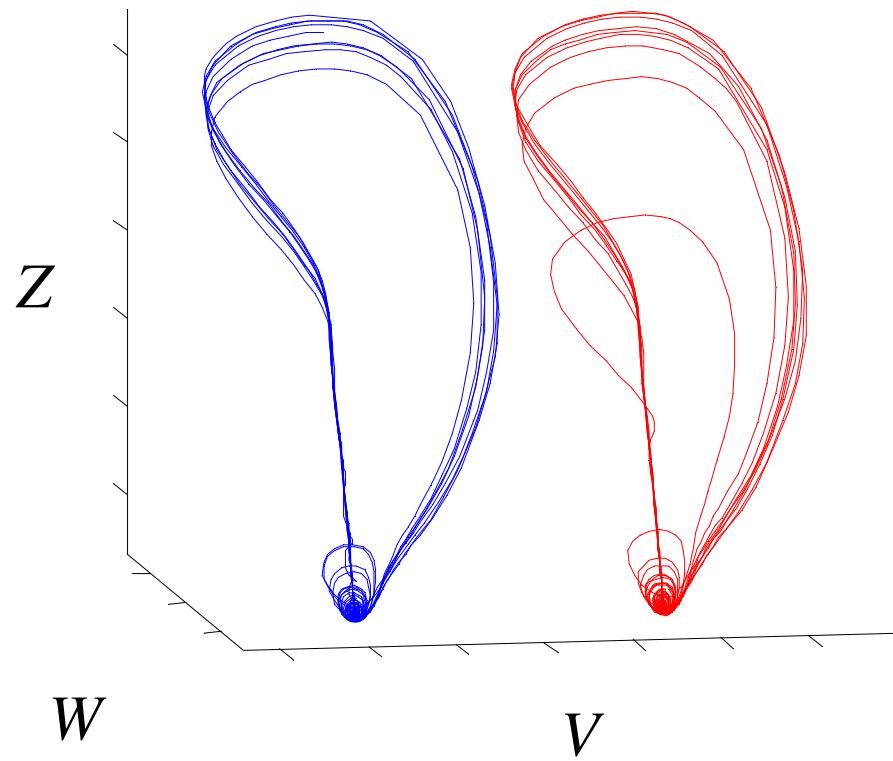
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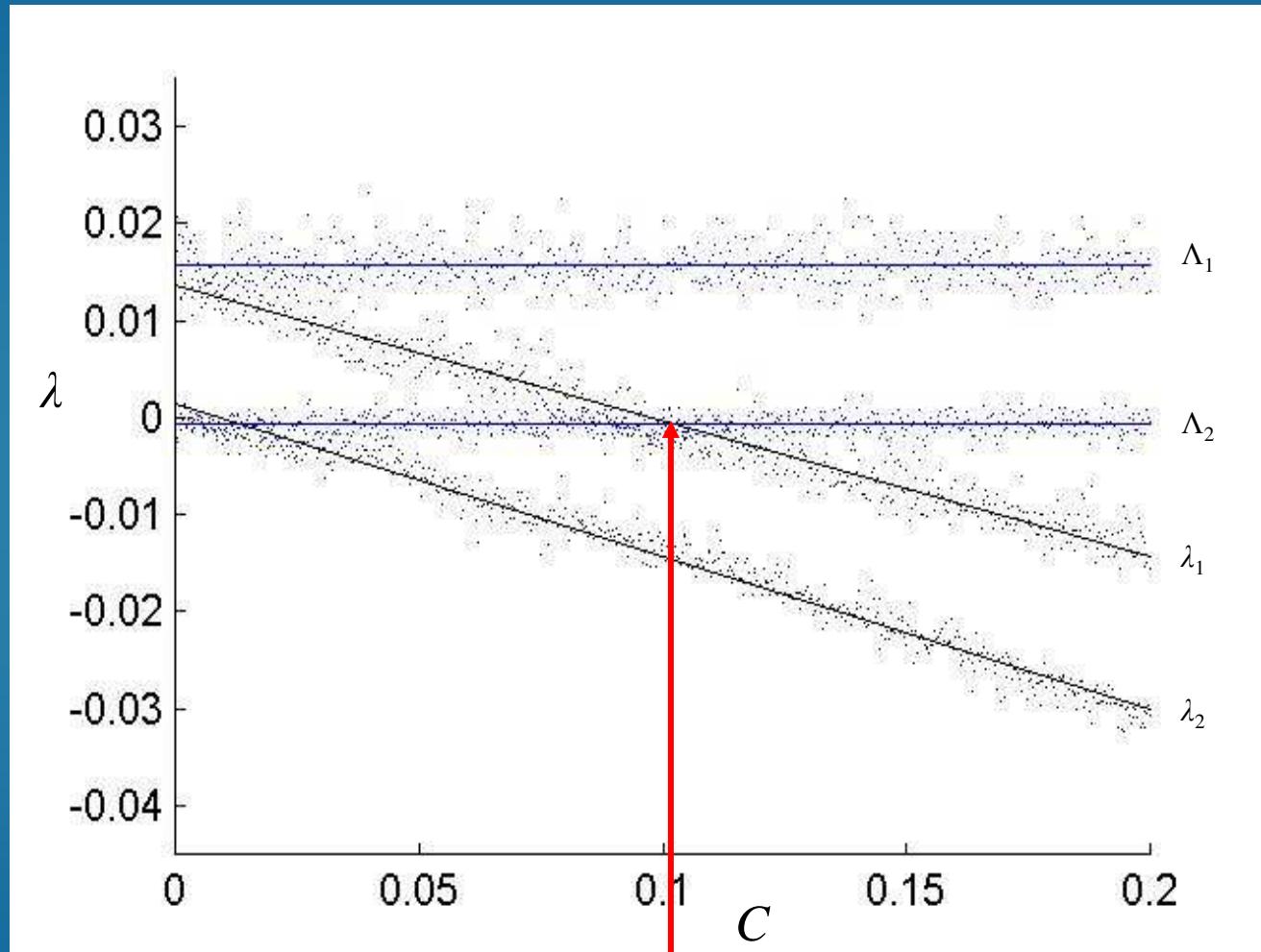
$V^i = V^j$: “Synchronization Manifold”

2. Nonlinear interdependence: Strong coupling

The dynamics can be divided into those within (\perp) and those transverse to (λ) the synchronization manifold.



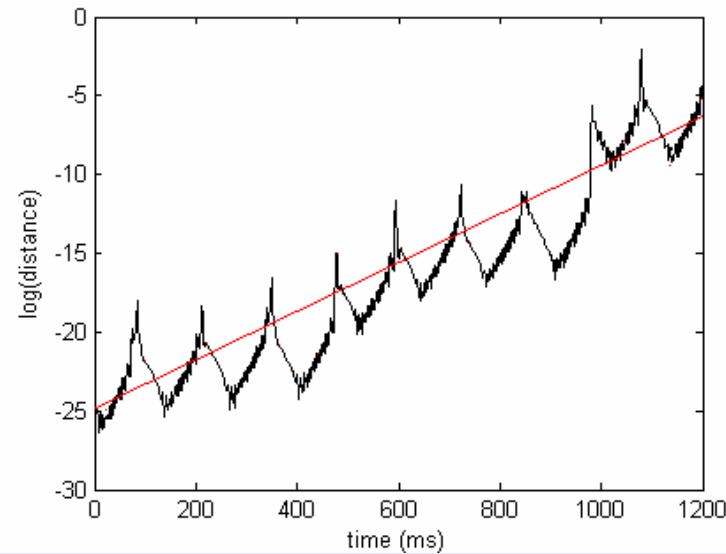
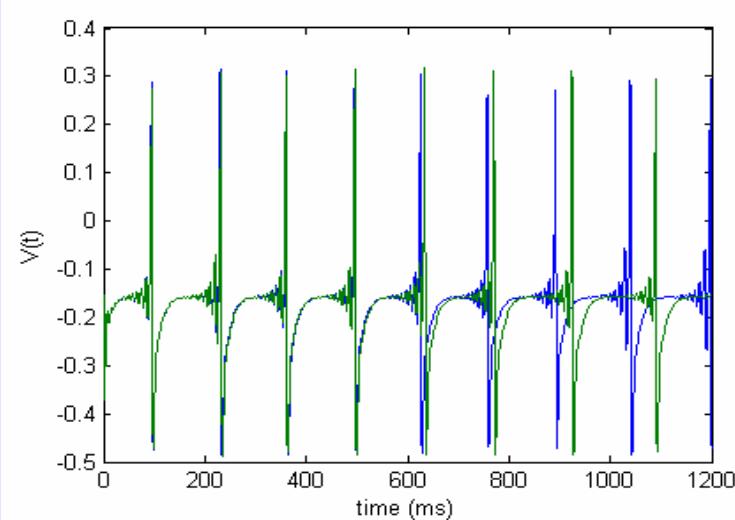
2. Nonlinear interdependence: Lyapunov spectra



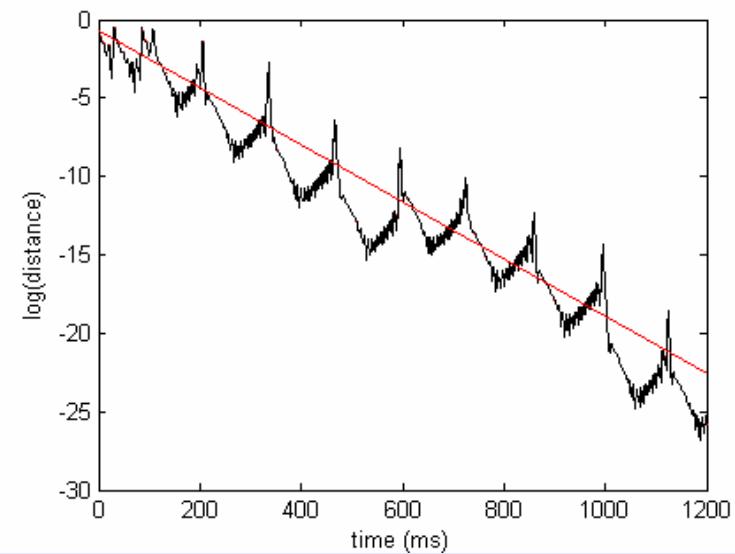
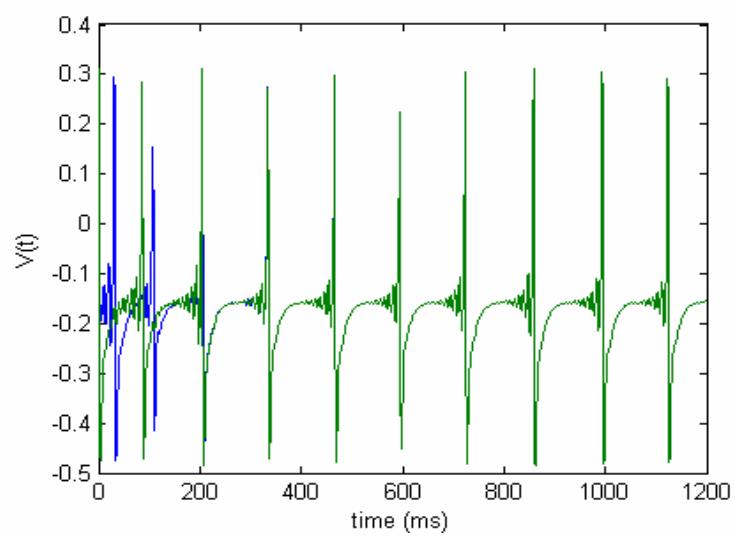
‘blowout’ bifurcation (Ott, Sommerer 1994)

2. Nonlinear interdependence: Lyapunov spectra

$C=0$

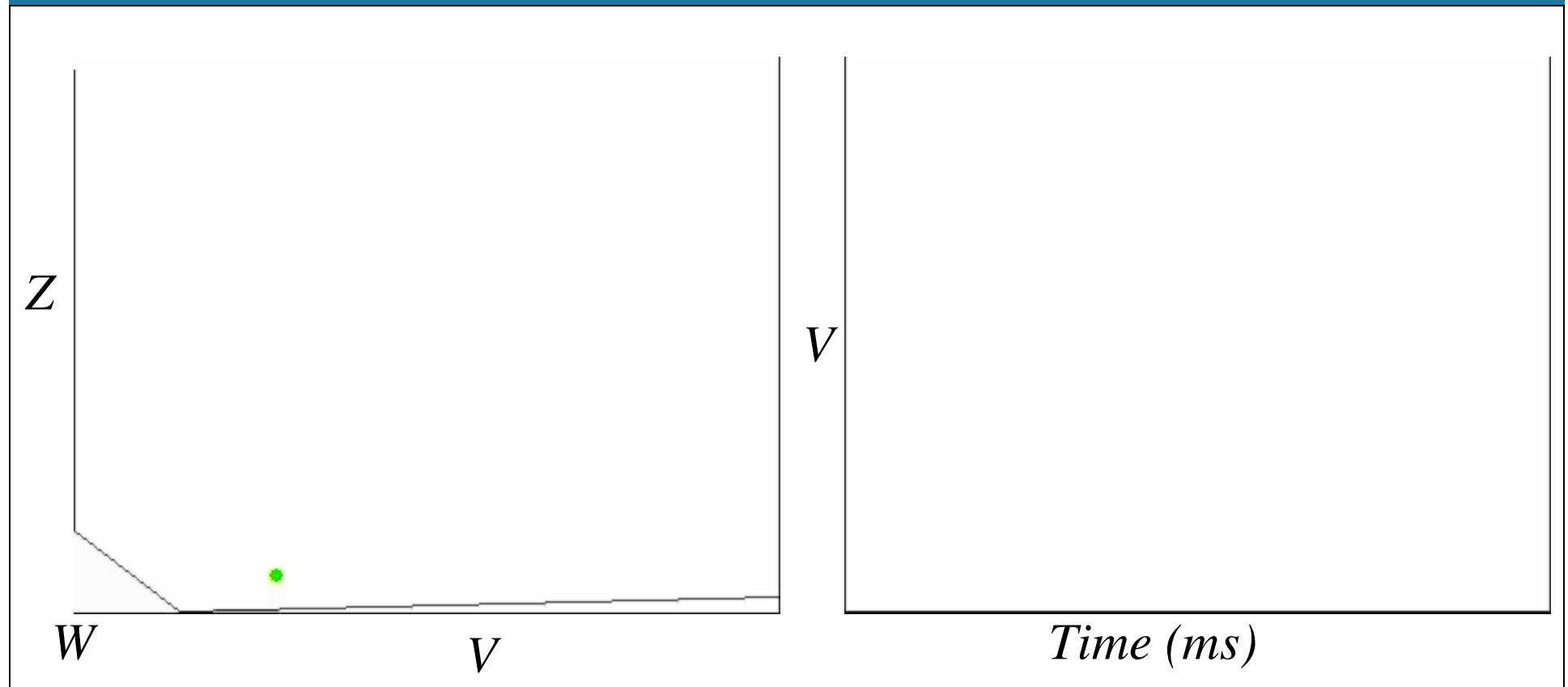


$C=0.2$



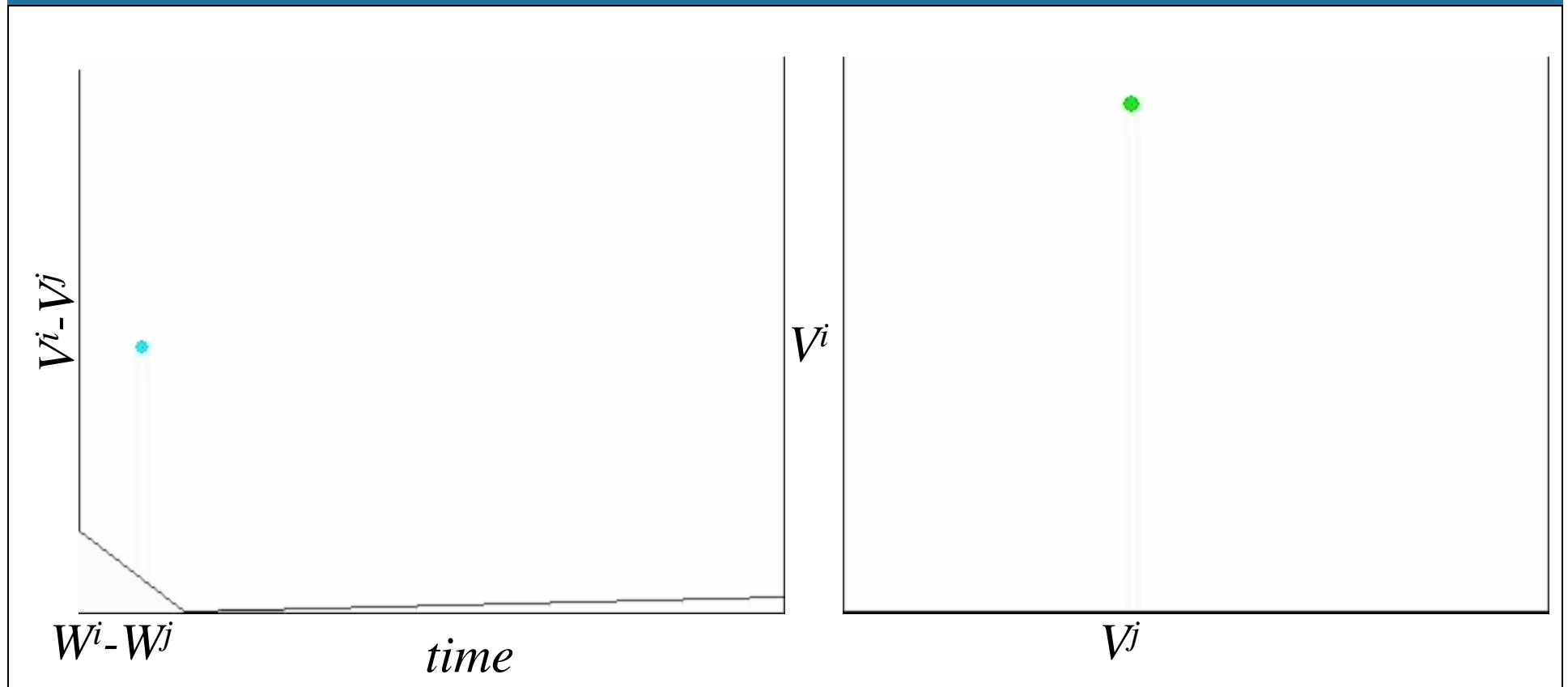
3. Nonlinear desynchronization

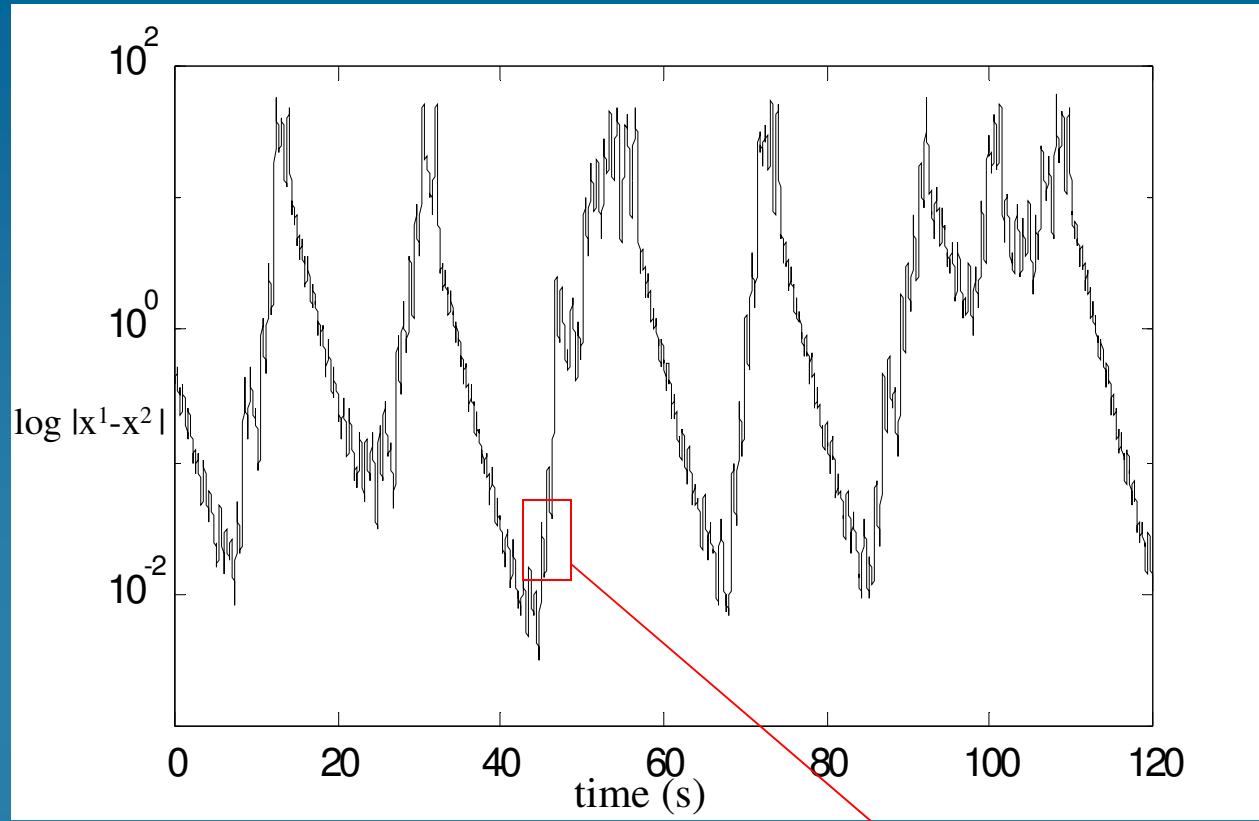
With weak coupling ($C=0.05$), the systems exhibit intermittent desynchronizations



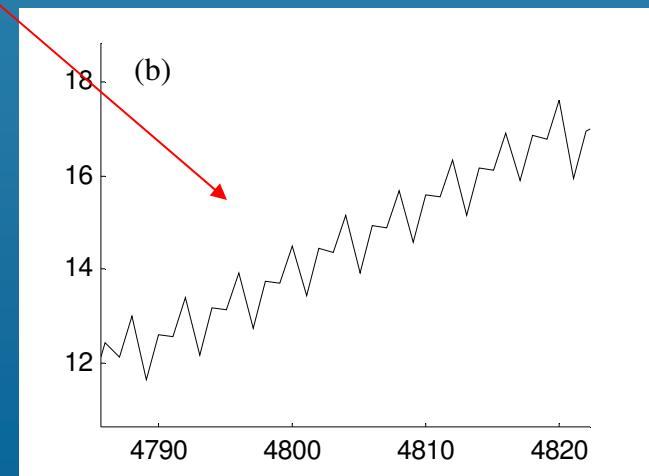
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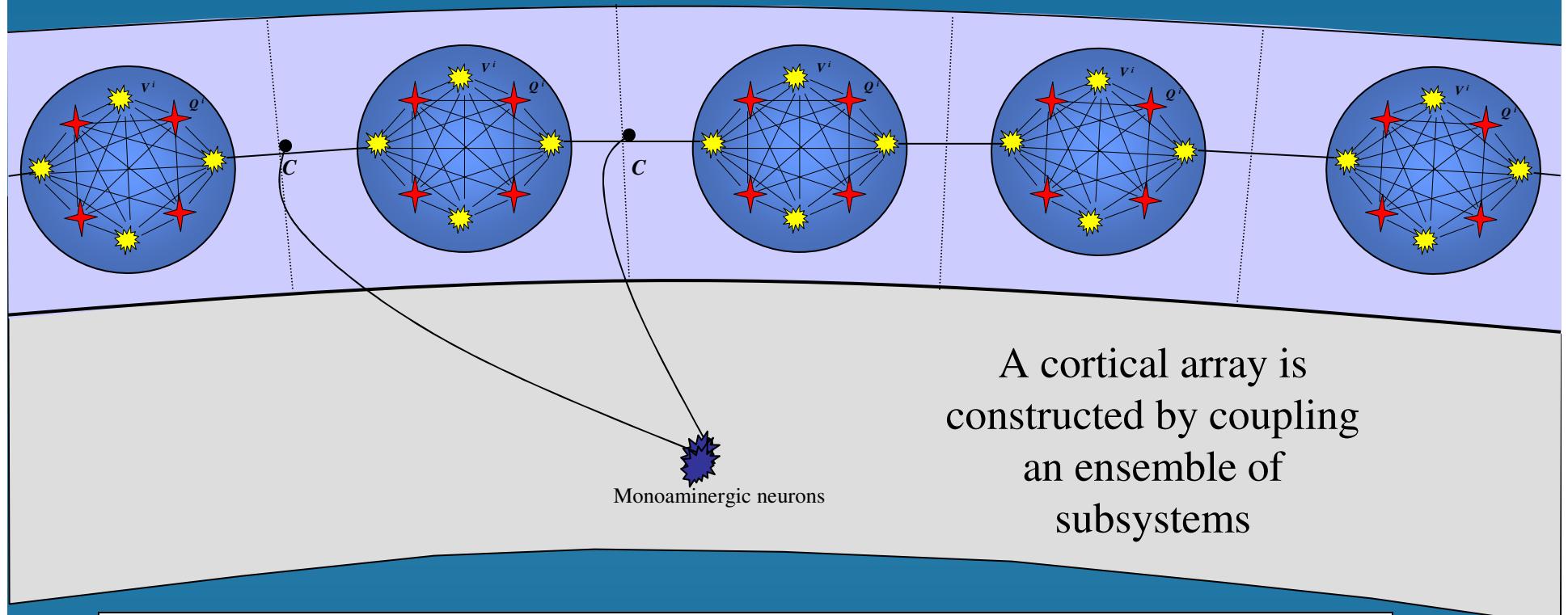




Low order periodic orbits are
the least stable

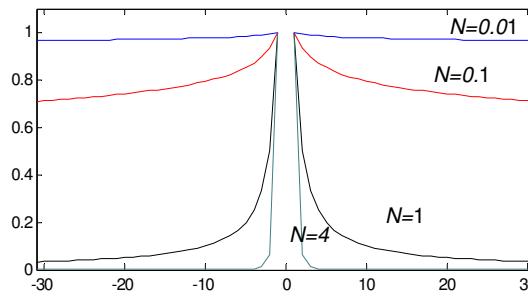


4. Cortical Arrays

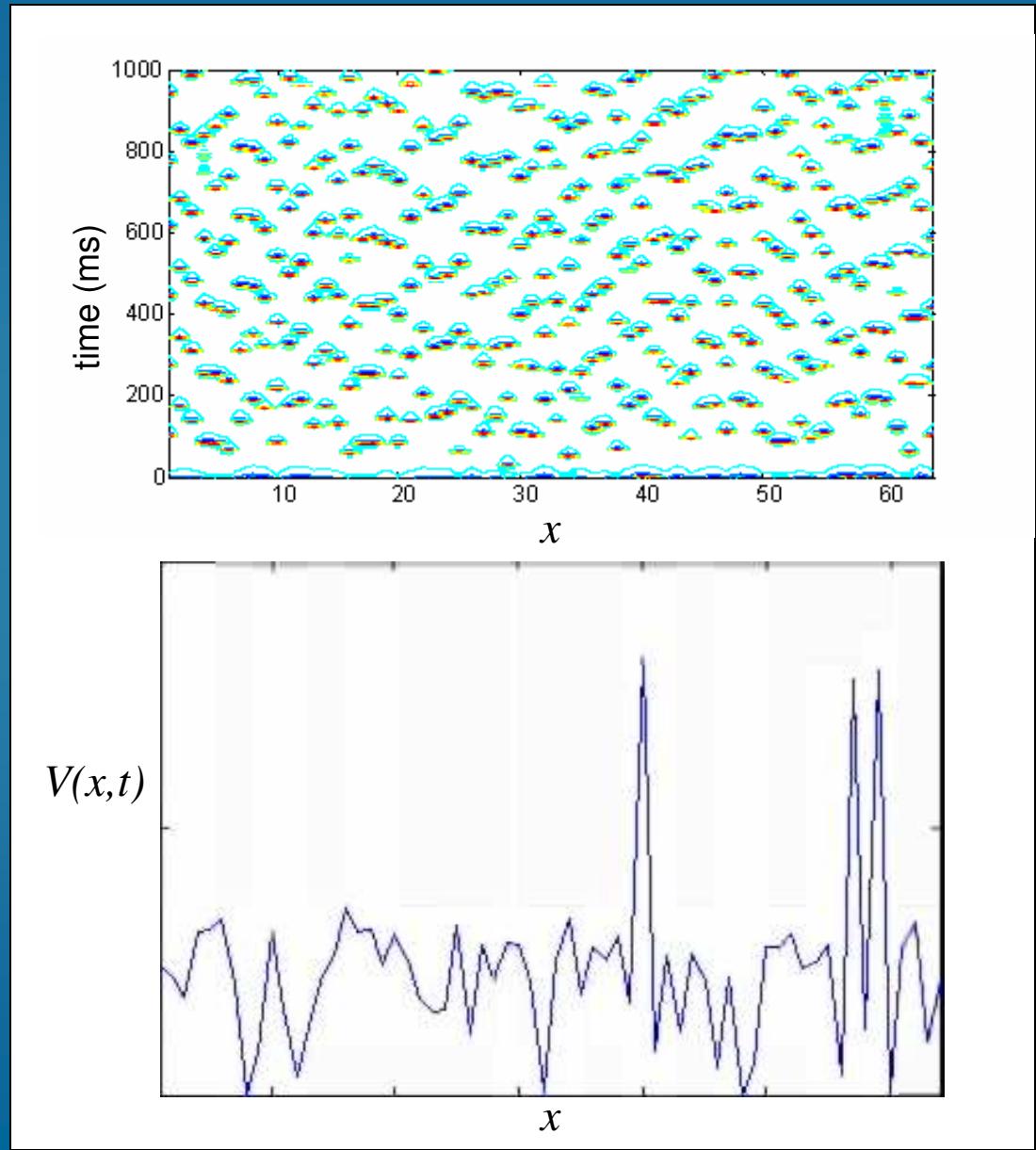
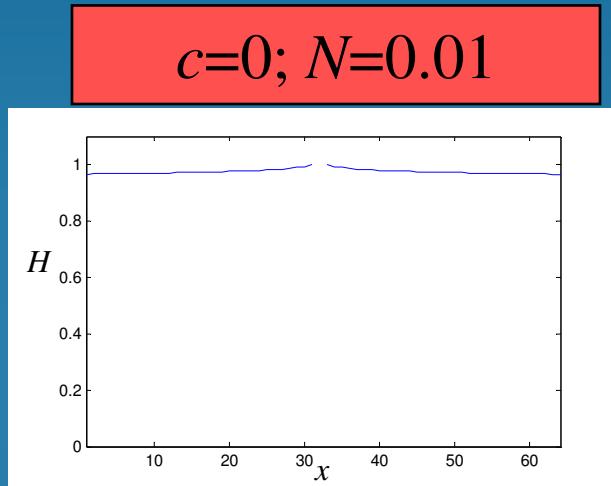


The strength of the coupling drops inversely with subsystem separation

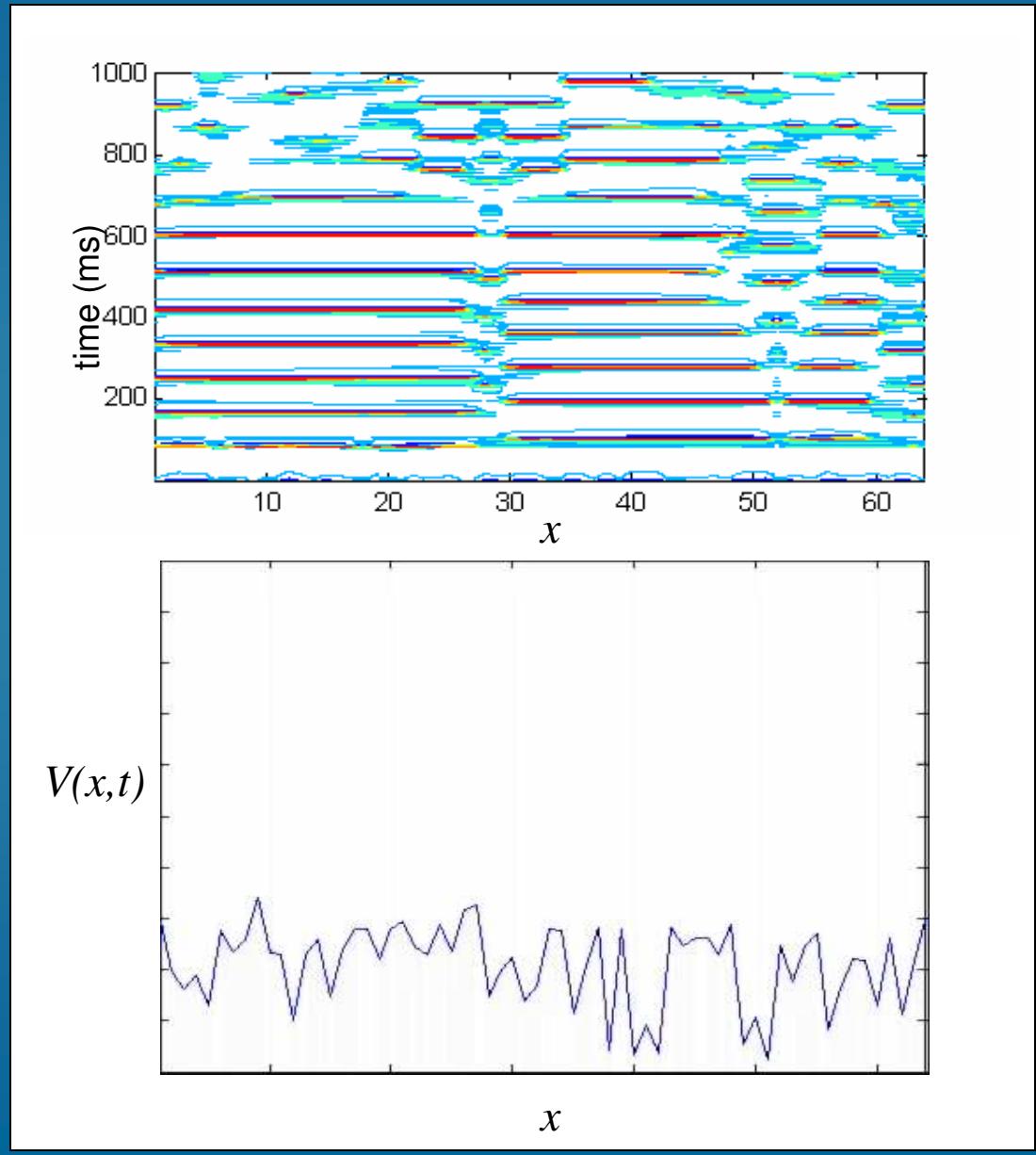
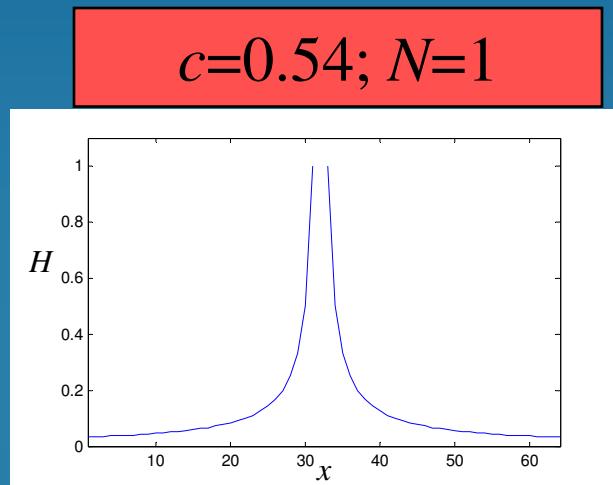
$$H(i, j) = \frac{K}{|\mathbf{x}_i - \mathbf{x}_j|^N}.$$



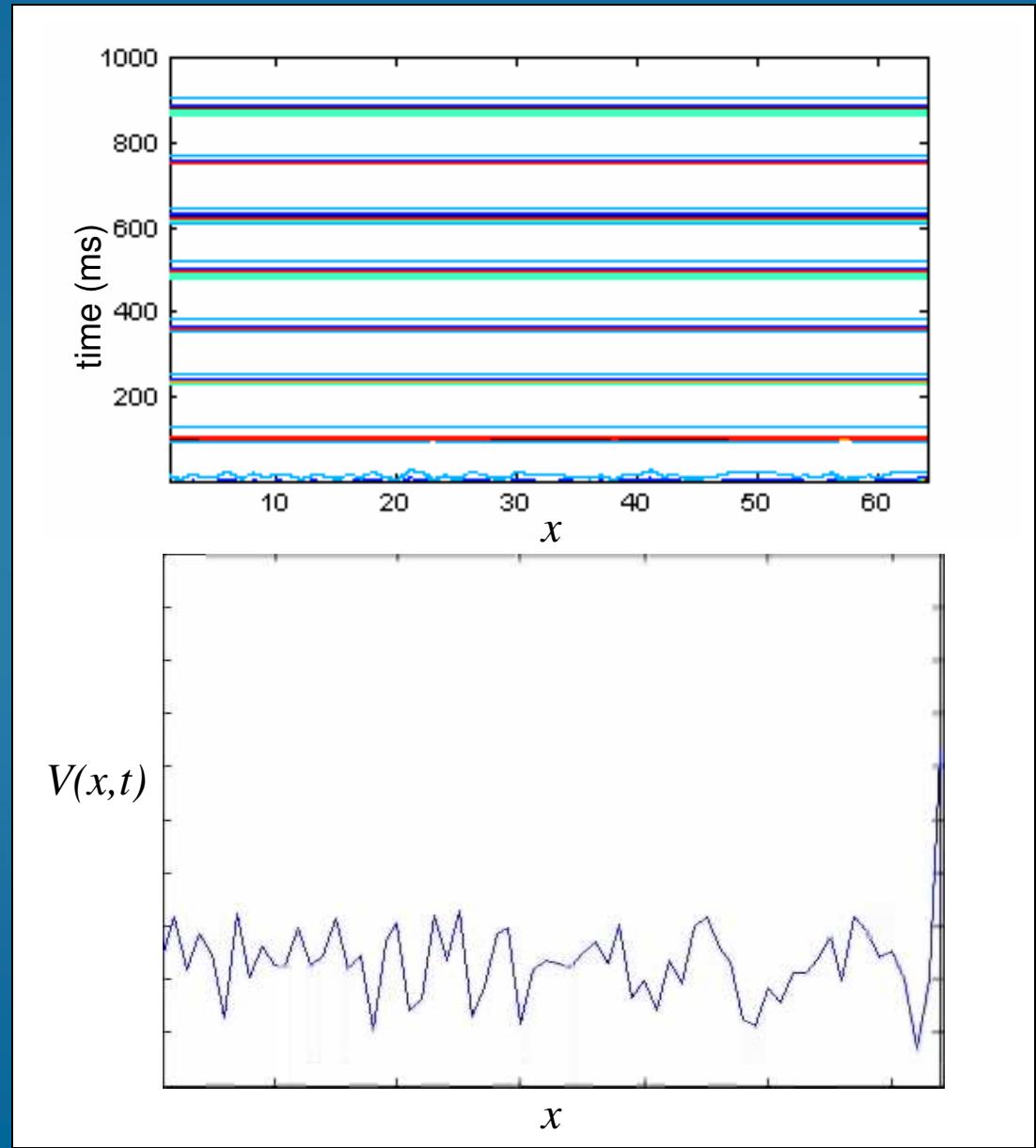
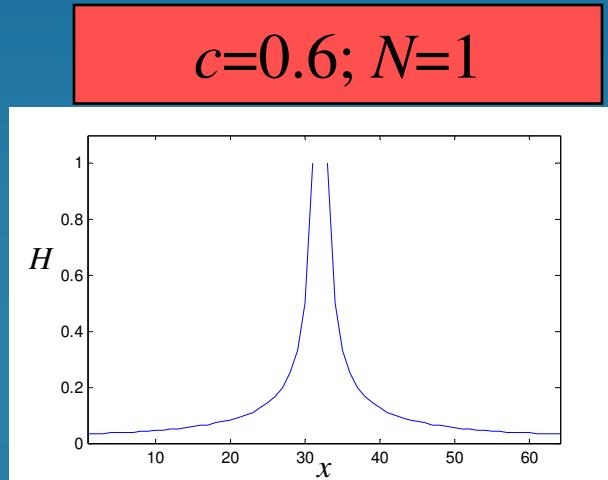
4. Cortical Arrays



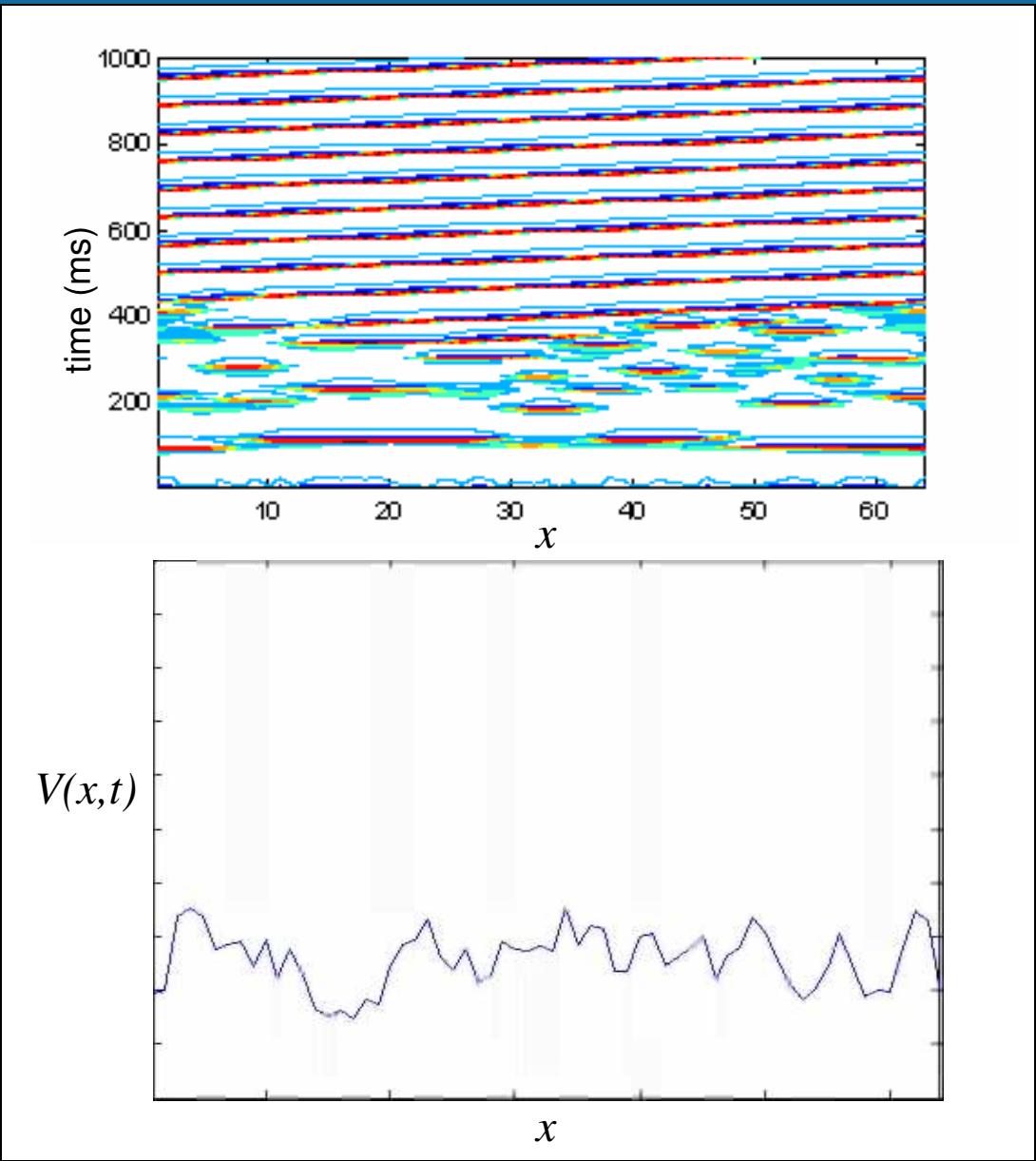
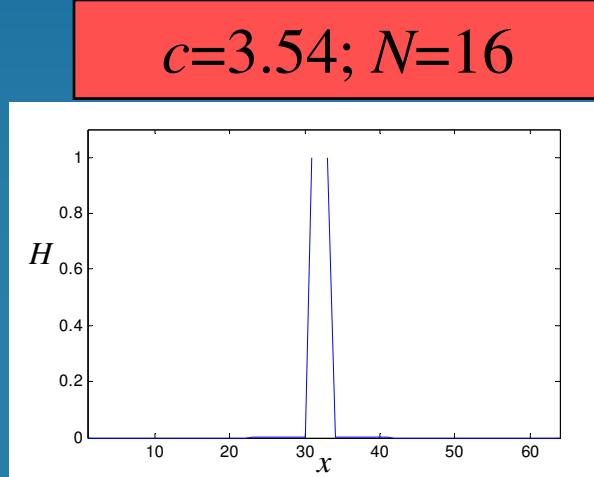
4. Cortical Arrays



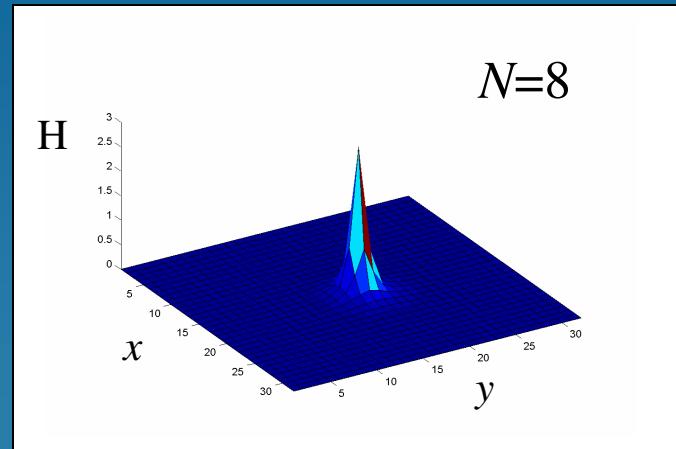
4. Cortical Arrays



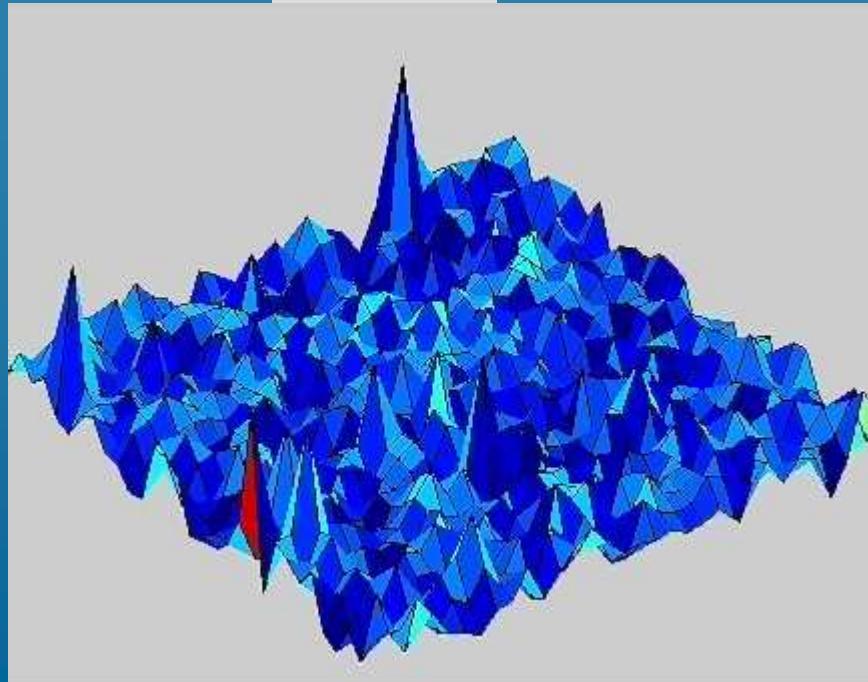
4. Cortical Arrays



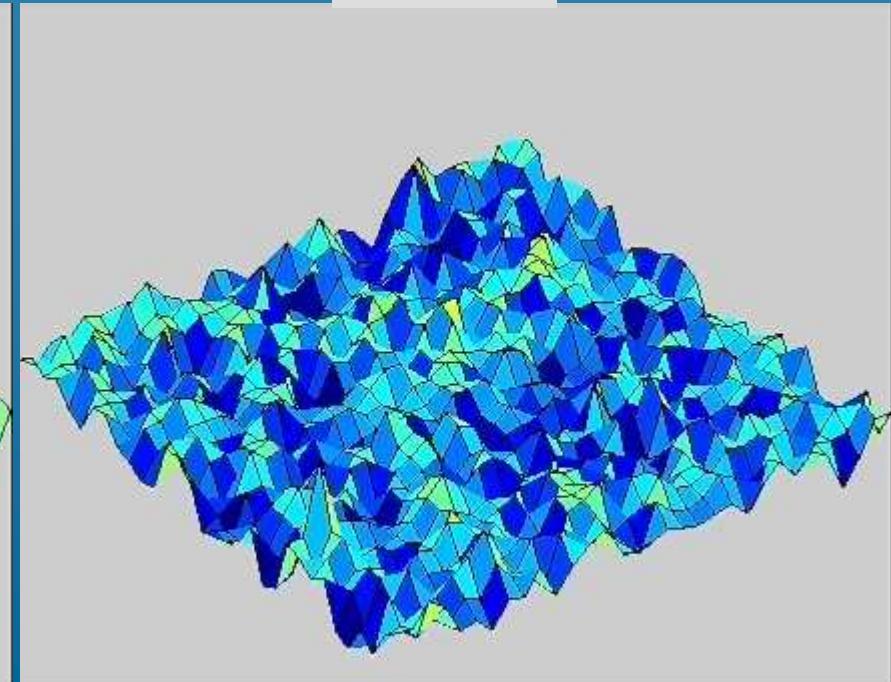
4. Cortical Arrays: 2-D



$c=0.5$



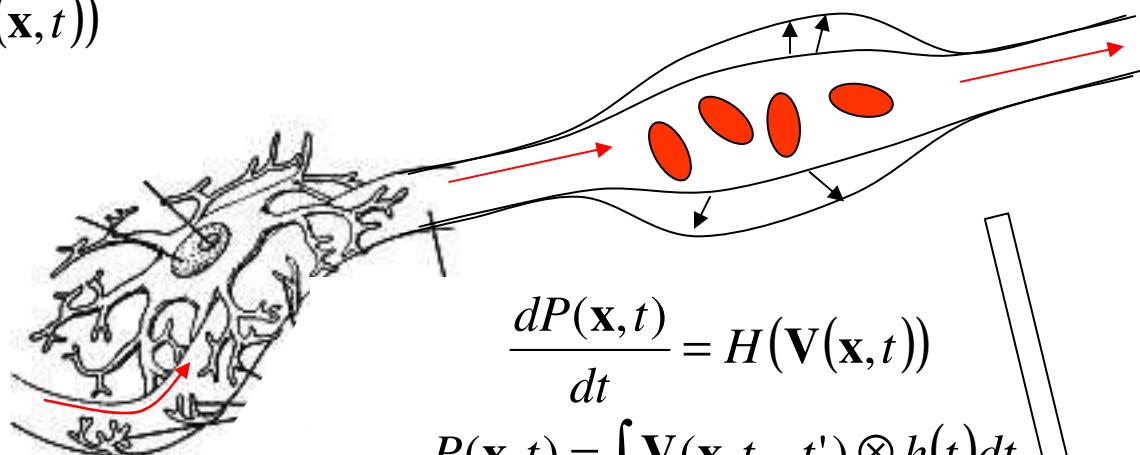
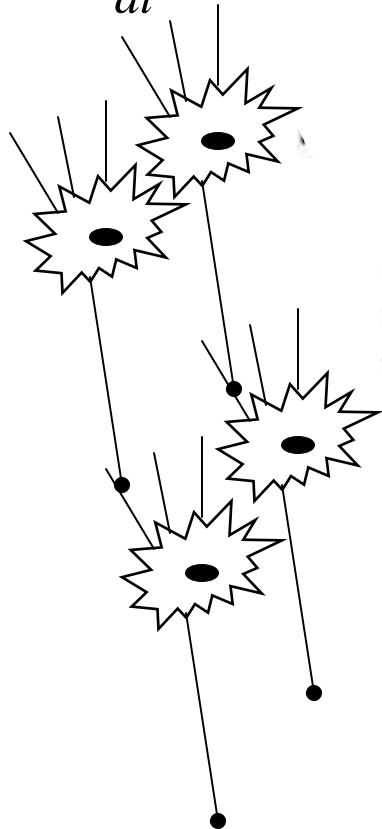
$c=1$



5. From model to data: Haemodynamic convolution

Neural activity, $\mathbf{V}(\mathbf{x}, t)$ \longrightarrow Physiological process, $P(\mathbf{x}, t)$

$$\frac{d\mathbf{V}(\mathbf{x}, t)}{dt} = F(\mathbf{V}(\mathbf{x}, t))$$



$$\frac{dP(\mathbf{x}, t)}{dt} = H(\mathbf{V}(\mathbf{x}, t))$$

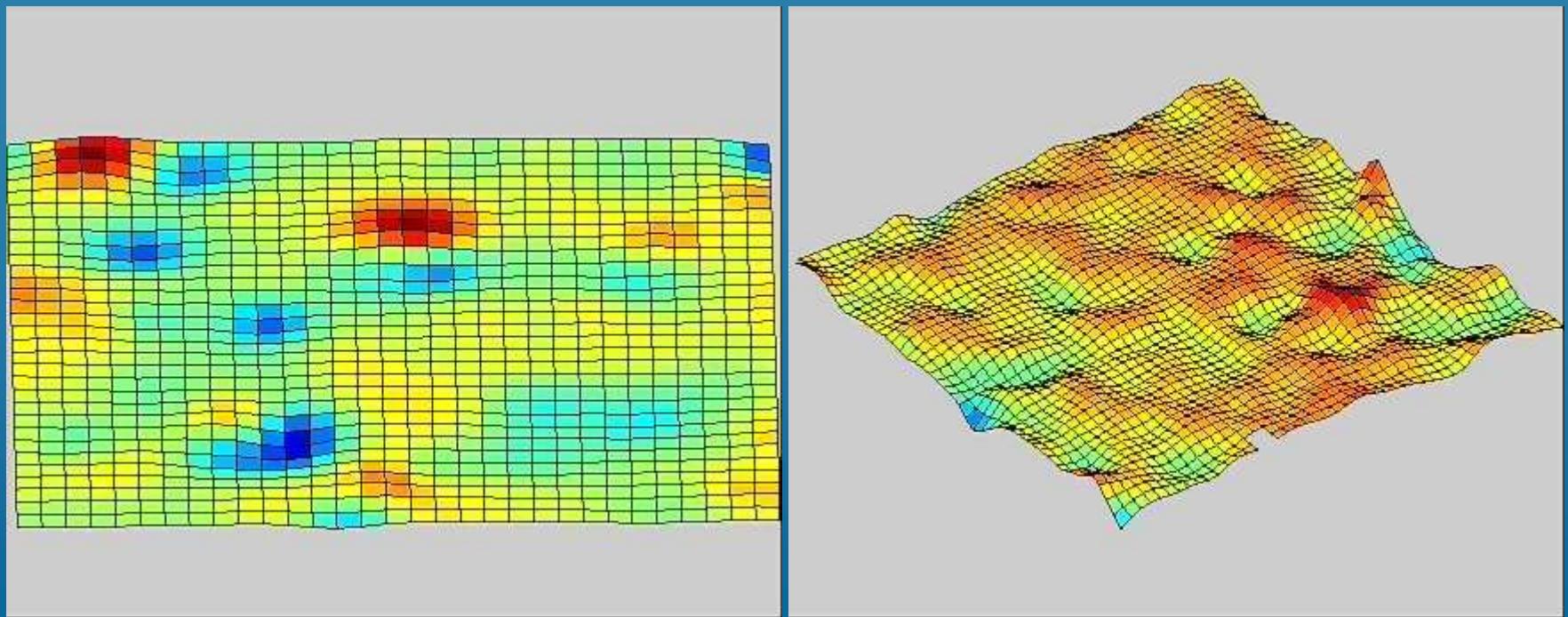
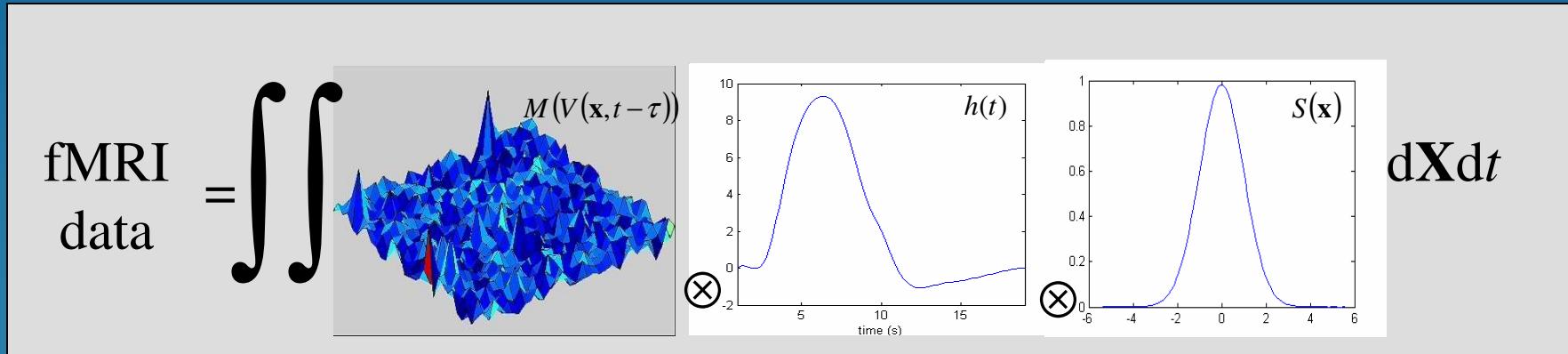
$$P(\mathbf{x}, t) = \int_{\Omega} \mathbf{V}(\mathbf{x}, t - t') \otimes h(t') dt'$$

Experimental signal, $s_k(t_k)$

$$S_k(x_i, t_i) = \int_{\Omega} P(\mathbf{x} - \mathbf{x}', t) \otimes S(\mathbf{x}') d\mathbf{x}$$



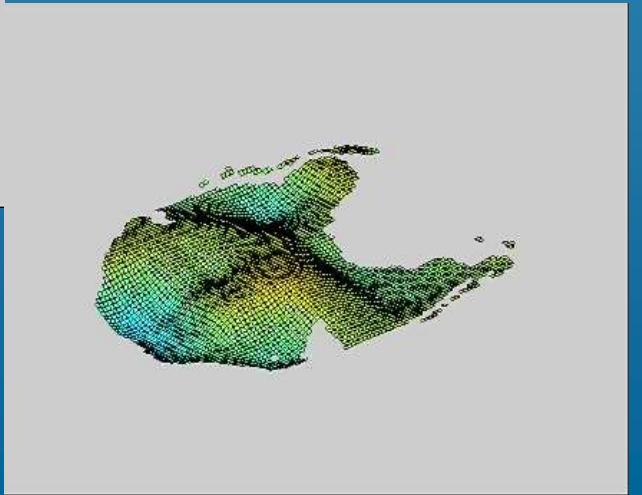
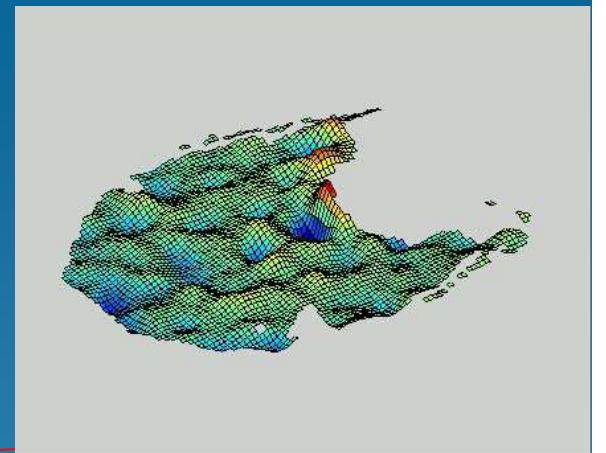
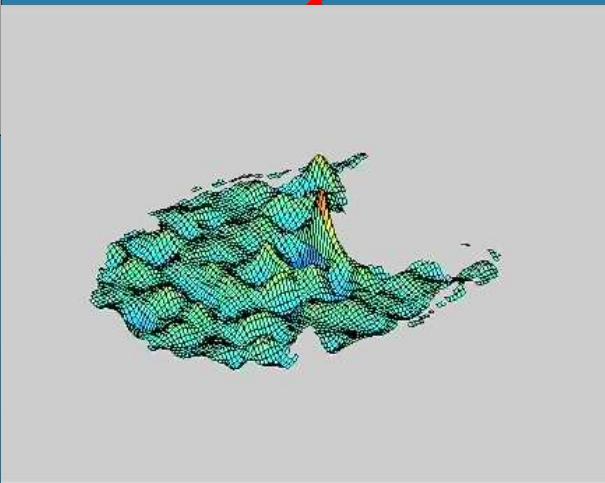
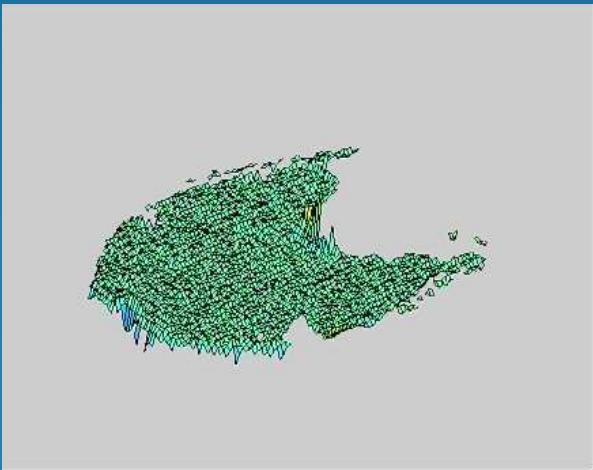
5. From model to data: Haemodynamic convolution



Simulated fMRI data

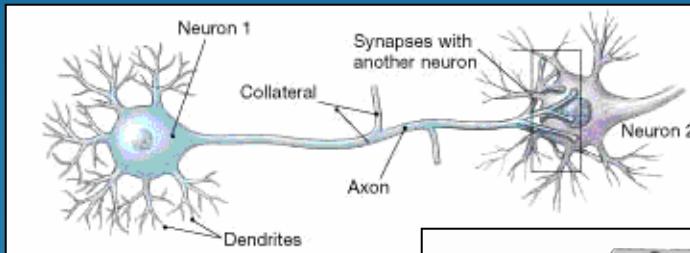
Observed fMRI data

II: Wavelets

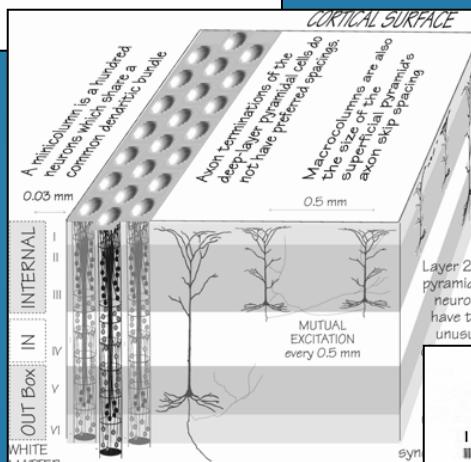


Wavelets permit the measurement
and modelling of inter-scale effects
in neural systems

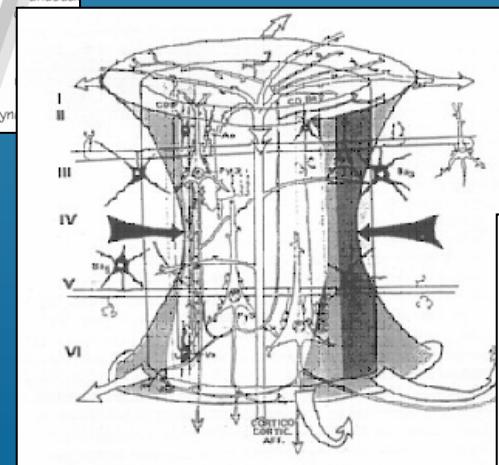
The modular architecture of the neuropil is a key feature of neural organization



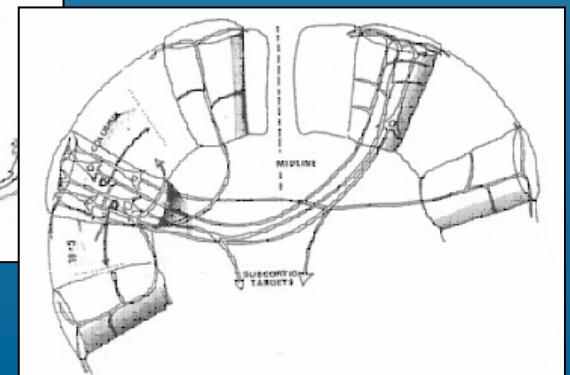
Microscopic



This modular architecture is apparent over a hierarchy of spatial scales

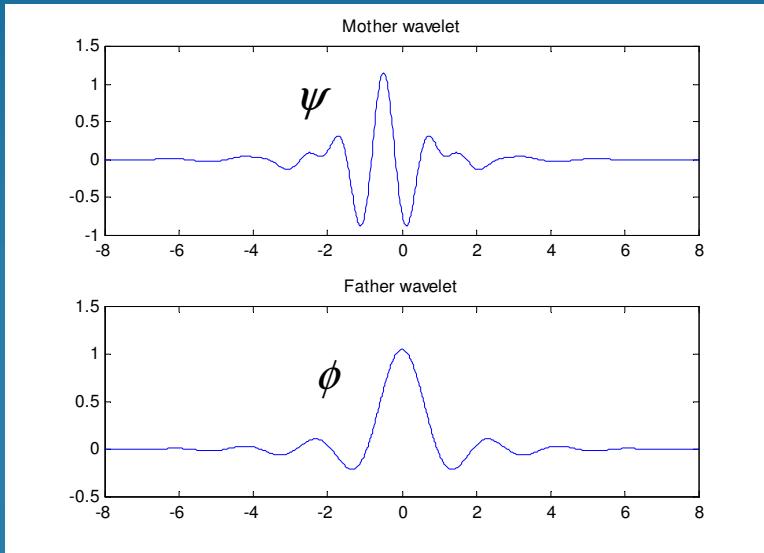


Macroscopic



How does information “cascade” from microscopic feature-specific neurons/networks to macroscopic cortical regions?

Wavelets are natural basis functions for investigating such phenomena



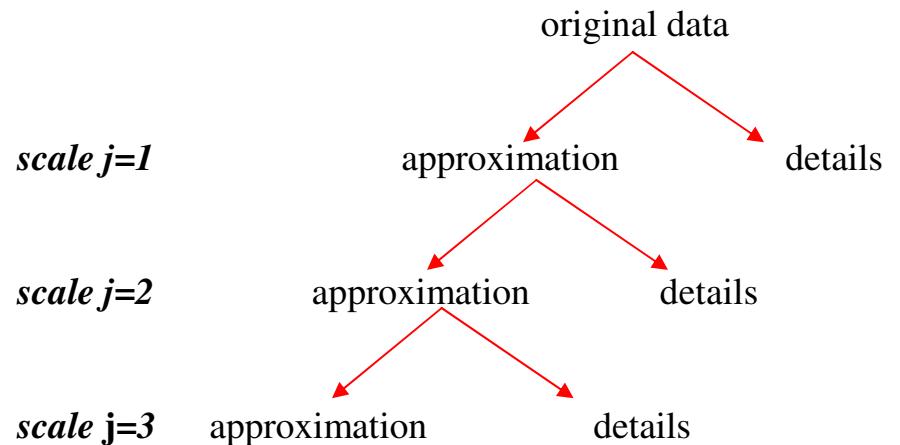
Wavelets

Wavelets are families of functions generated from a single ‘mother’ wavelet function ψ by,

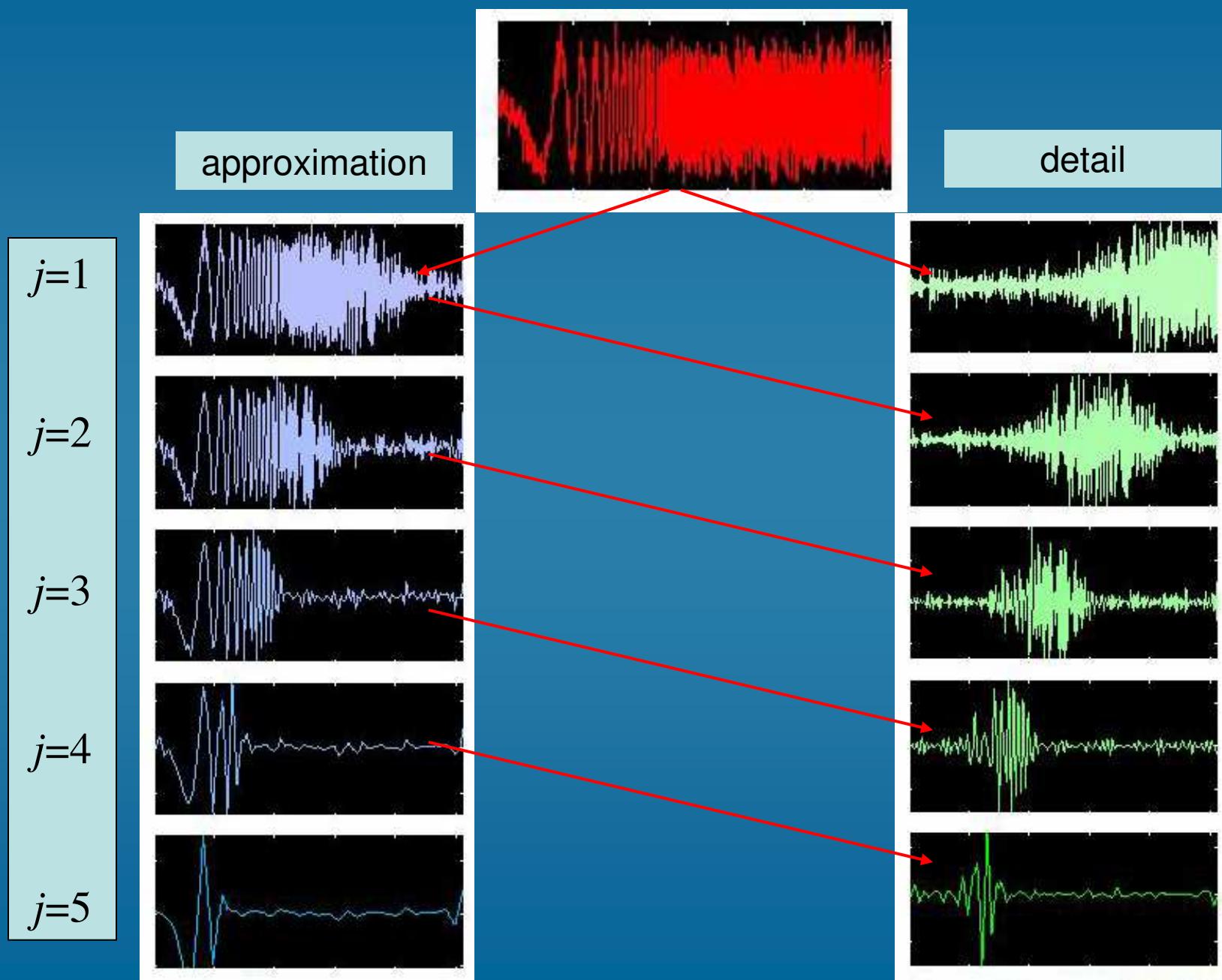
$$\psi^{j,k}(\mathbf{x}) = \frac{1}{\sqrt{2^j}} \psi\left(\frac{\mathbf{x} - 2^j k}{2^j}\right), \quad j, k \in \mathbb{Z}.$$

where j denotes ‘scale’ and k ‘position’

Wavelets (and their cousins, “scaling” functions) permit a “multiscale decomposition” of any signal across a hierarchy of scales $j=1,2,3, \dots, N$



Wavelet decomposition of a ‘chirp’



Wavelet decomposition: Mathematical form

Properties

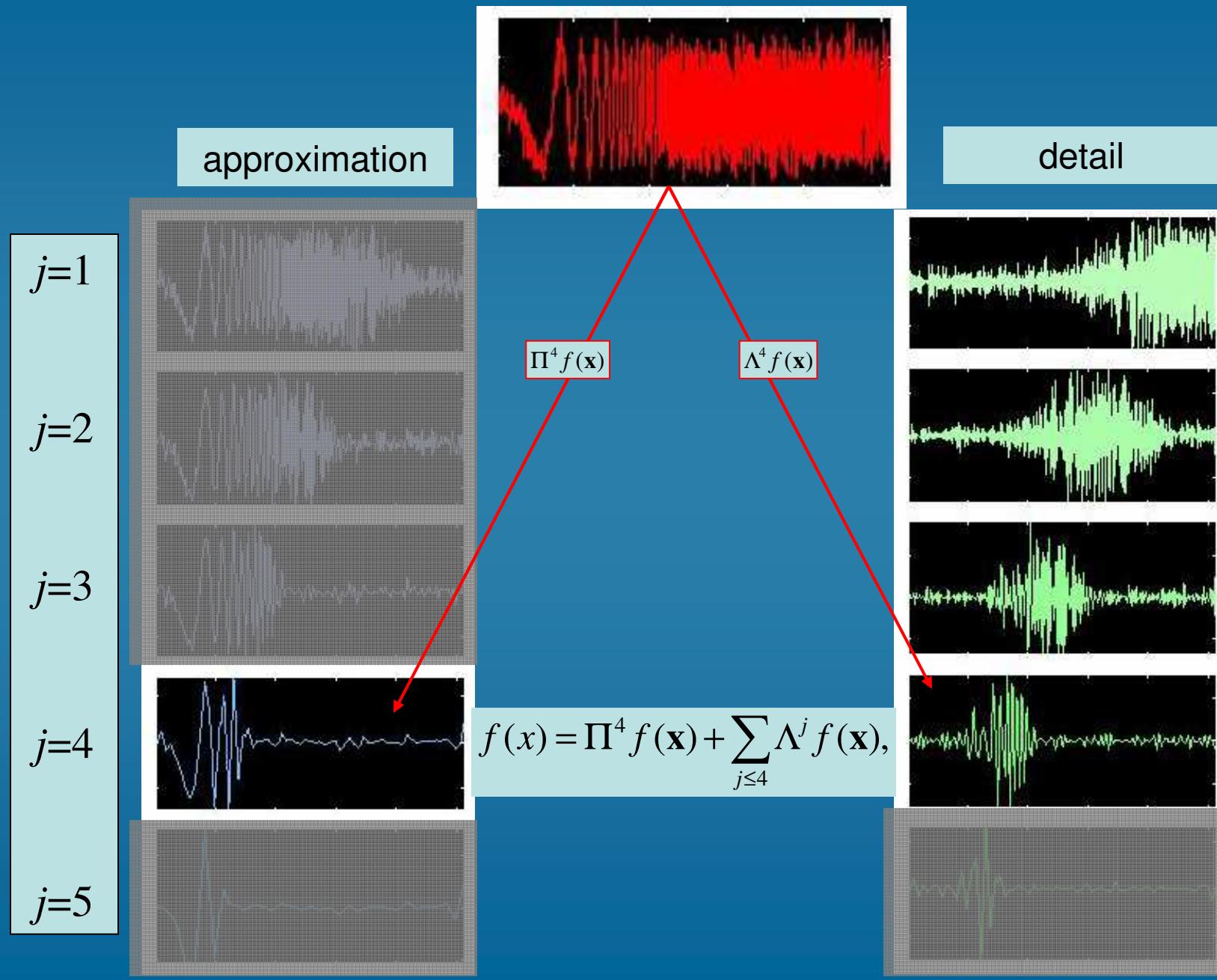
Let W be the linear subspace spanned by ψ^j and L^j be the subspace projector onto W^j . Then:

1. $f(\mathbf{x}) \in W \Leftrightarrow f(2\mathbf{x}) \in W^{j+1}$.
2. $\bigcap_{j \in \mathbb{Z}} W^j = L^2(\mathbb{R})$ and $\bigcup_{j \in \mathbb{Z}} W_j = \{0\}$.

$$3. \quad f(x) = \prod_{j=J}^0 f(\mathbf{x}) + \sum_{j \leq J} \Lambda^j f(\mathbf{x}),$$
$$= \sum_{k \in I} a^{J,k} \phi^{J,k} + \sum_{j \leq J} \sum_{k \in I} d^{j,k} \psi^{j,k}.$$

where $d_{j,k} = \int f(\mathbf{x}) \psi_{j,k}(\mathbf{x}) d\mathbf{x}$.

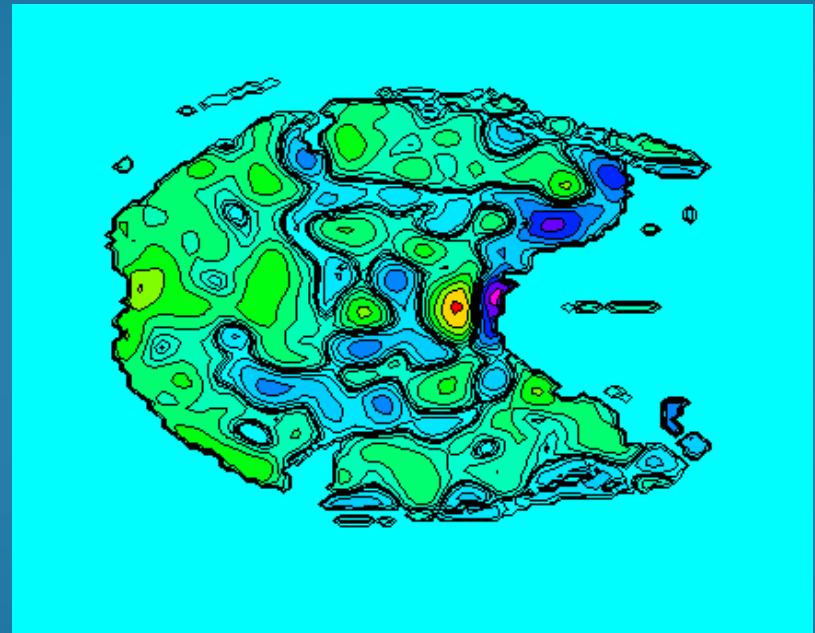
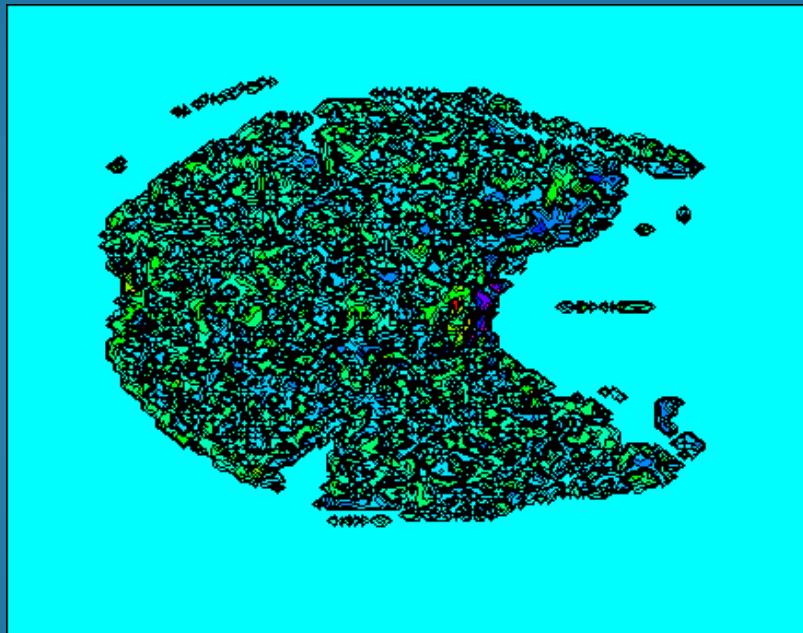
Wavelet decomposition of a ‘chirp’



1. Wavelet decomposition of fMRI data

$$Y(\mathbf{x}_1, t)$$

$$Y'(\mathbf{x}, t) = \int_{\Omega} G(\mathbf{x}) Y(\mathbf{x} - \mathbf{x}') d\mathbf{x}'$$

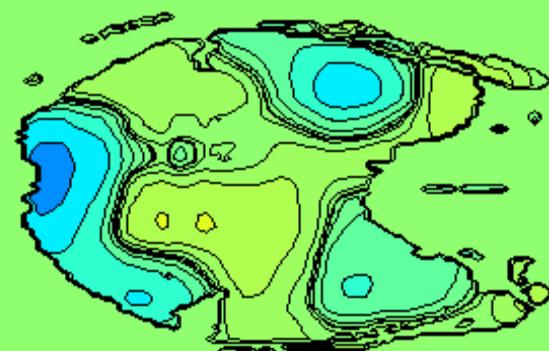
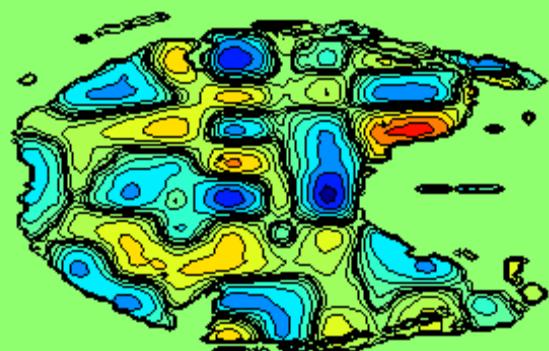
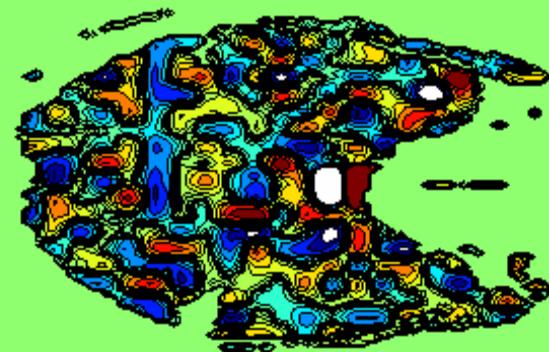


1. Wavelet decomposition of fMRI data

$$\Lambda^1 Y(\mathbf{x}, t)$$



$$\Lambda^3 Y(\mathbf{x}, t)$$



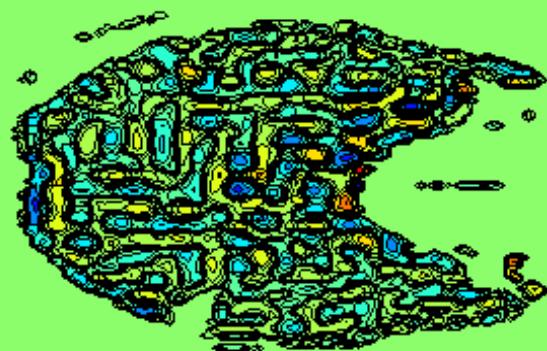
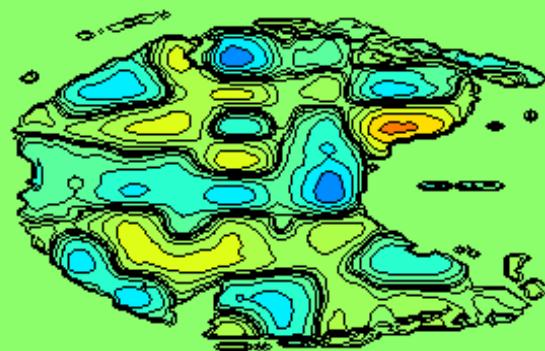
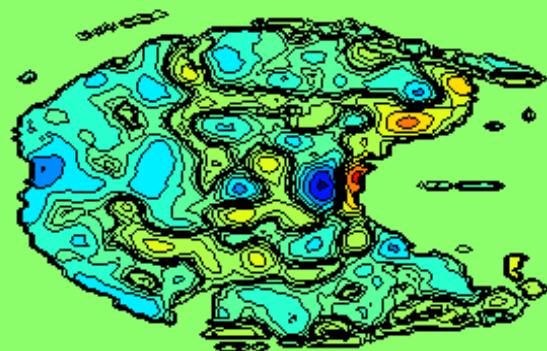
$$\Lambda^4 Y(\mathbf{x}, t)$$

$$\Lambda^5 Y(\mathbf{x}, t)$$

1. Wavelet decomposition of fMRI data

$$Y'(\mathbf{x}_1, t) = \int_{\Omega} G(\mathbf{x}) Y(\mathbf{x}_1 - \mathbf{x}) d\mathbf{x}$$

$$\Lambda^3 Y(\mathbf{x}, t)$$



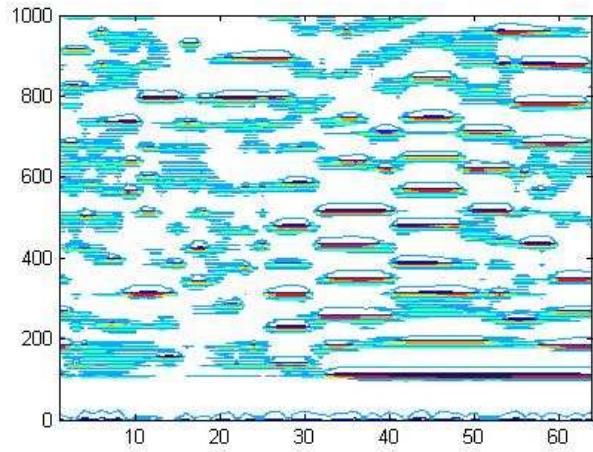
$$\Lambda^2 Y(\mathbf{x}, t)$$

$$\Lambda^5 Y(\mathbf{x}, t)$$



2. Multiscale connectivity in a neural model

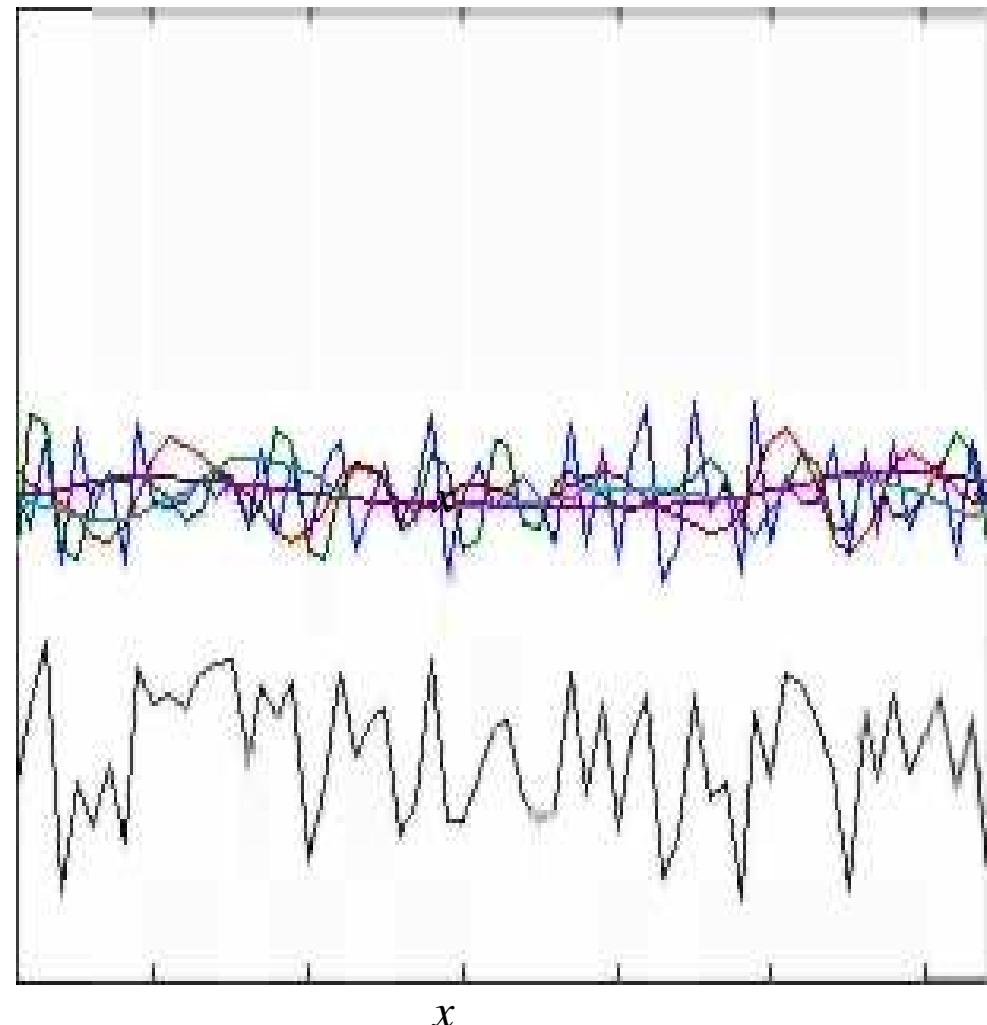
$c=3; N=16$



$W_j V(x,t)$

Projection of $V(x,t)$ onto
orthogonal wavelet
subspaces $W_j V(x,t)$
 $j=1,2,\dots,5$

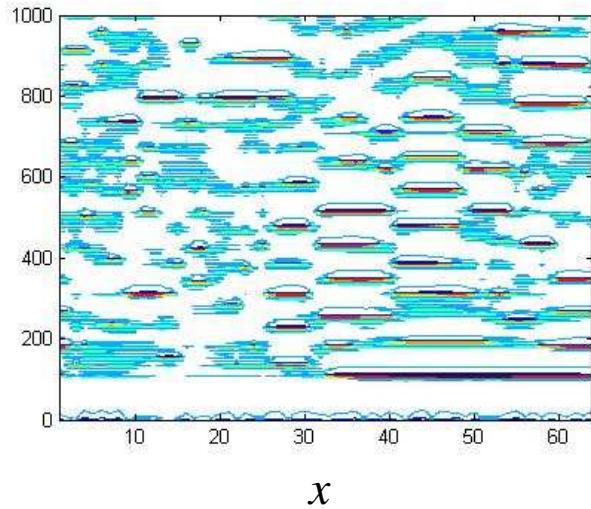
$V(x,t)$





2. Multiscale connectivity in a neural model

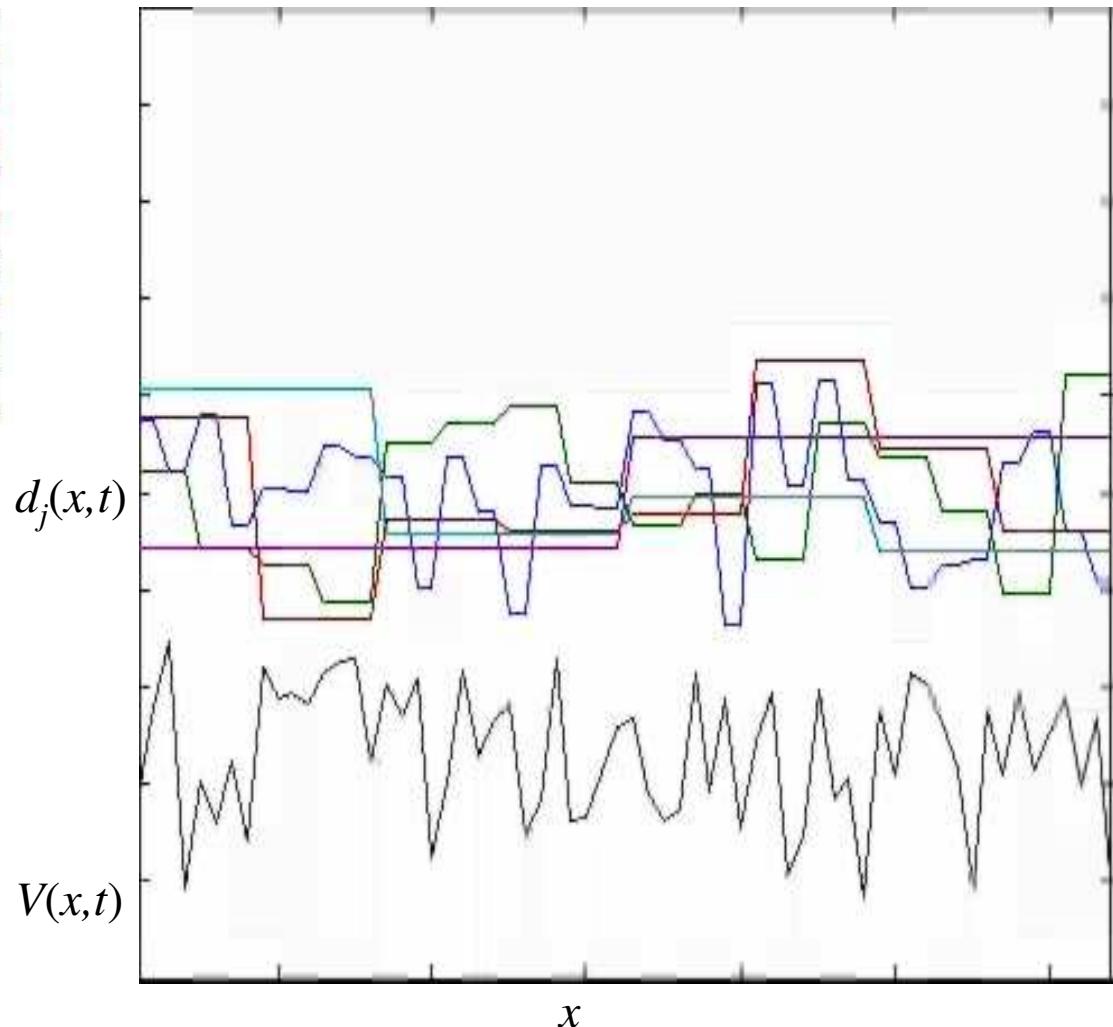
$c=3; N=16$



x

Convolution with
wavelet functions to
yield detail coefficients

$$d_{j,k} = \int f(\mathbf{x})\psi_{j,k}(\mathbf{x})d\mathbf{x},$$
$$j=1,2,\dots,5$$





2. Multiscale connectivity in a neural model

$c=3; N=16$

Taking the inner product $\langle f, g \rangle$ as,

$$\langle f(\mathbf{x}), g(\mathbf{x}) \rangle_I = \int_I f(\mathbf{x}).g(\mathbf{x})d\mathbf{x},$$

then define the cross-scale correlation function as,

$$\text{CC}_{j_1, j_2}(I, \Delta t) = \frac{\overline{\langle d_{j_1}(x, t).d_{j_2}(x, t + \Delta t) \rangle_I}}{\sqrt{\langle d_{j_1}(x, t).d_{j_1}(x, t) \rangle_I} \cdot \sqrt{\langle d_{j_2}(x, t + \Delta t).d_{j_2}(x, t + \Delta t) \rangle_I}}.$$

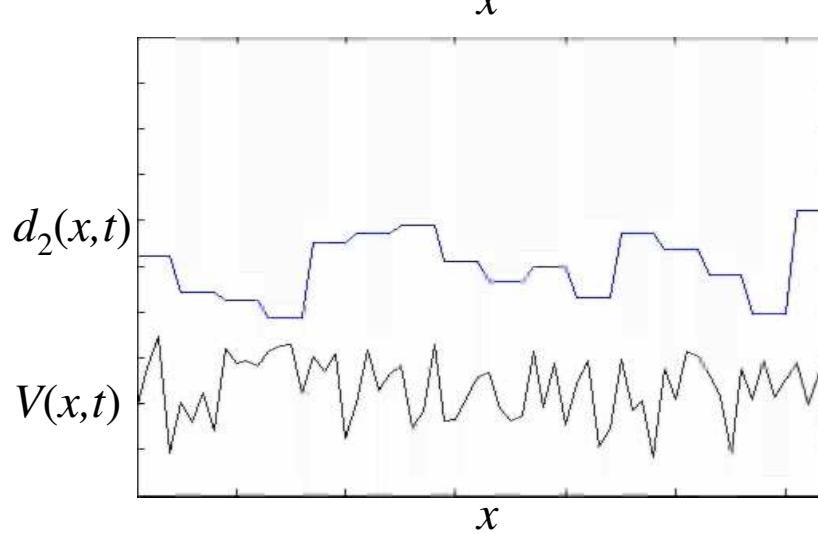
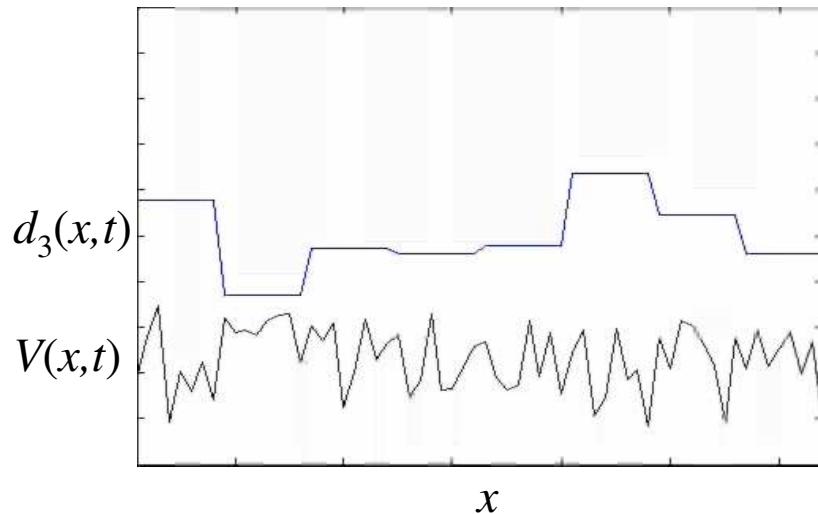
This can be decomposed into its time symmetric and anti-symmetric components,

$$\text{DD}_{j_1, j_2}(I, \Delta t) = \frac{\text{CC} + \text{CC}^T}{2},$$

$$\text{EE}_{j_1, j_2}(I, \Delta t) = \text{CC} - \text{CC}^T.$$

Note that $\text{EE}(I, 0) = 0$: Hence **EE** can be interpreted as information ‘flow’ between scales

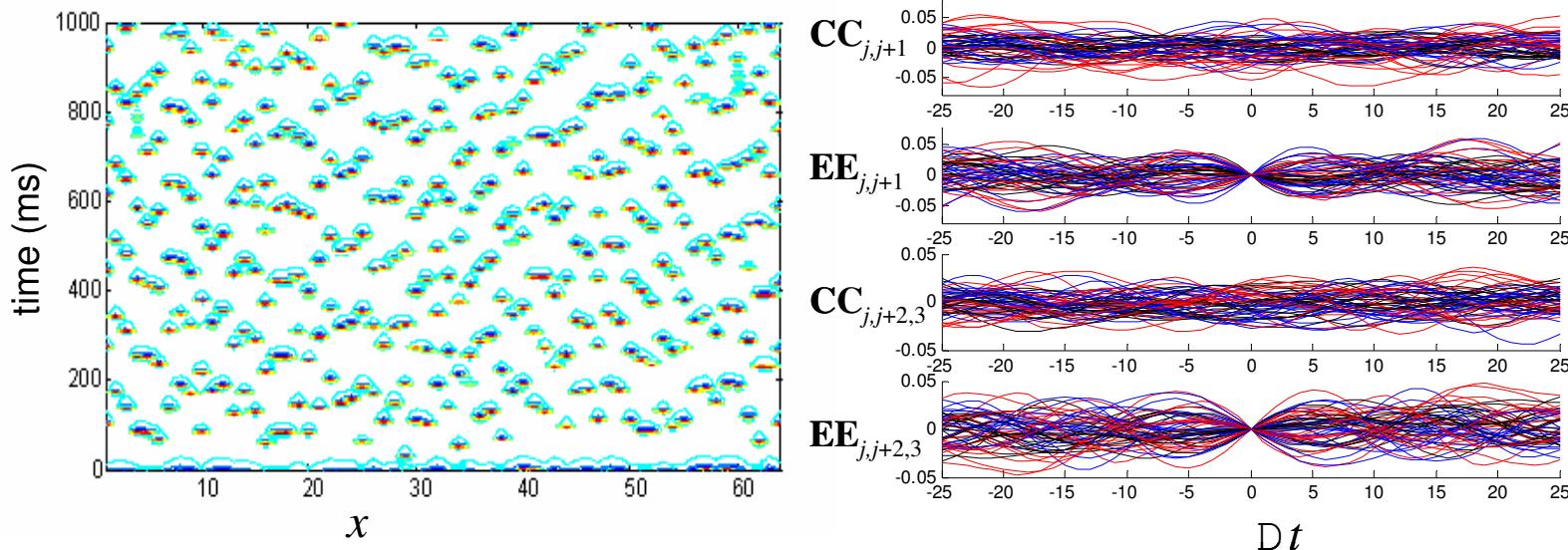
from (Nakao *et al.* 2001 IJBC 11: 1483)





2. Multiscale connectivity in a neural model

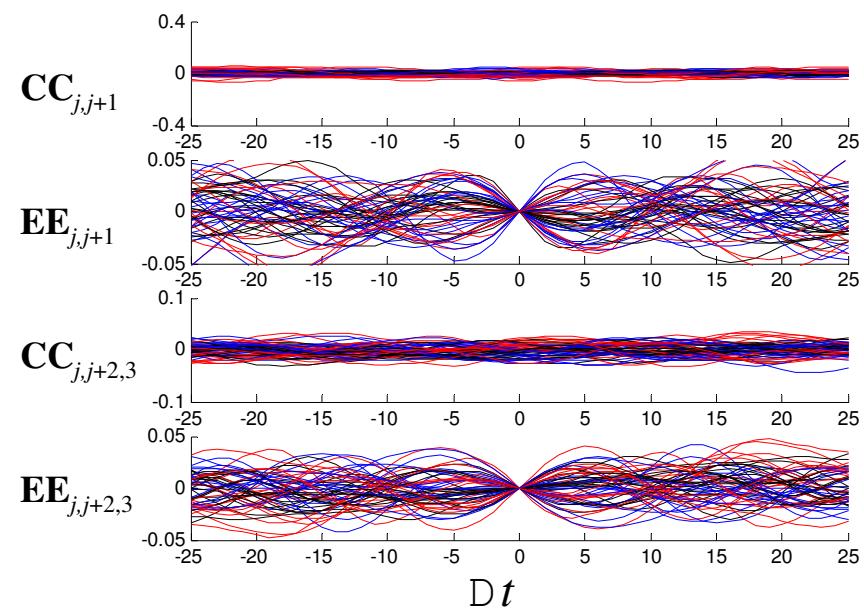
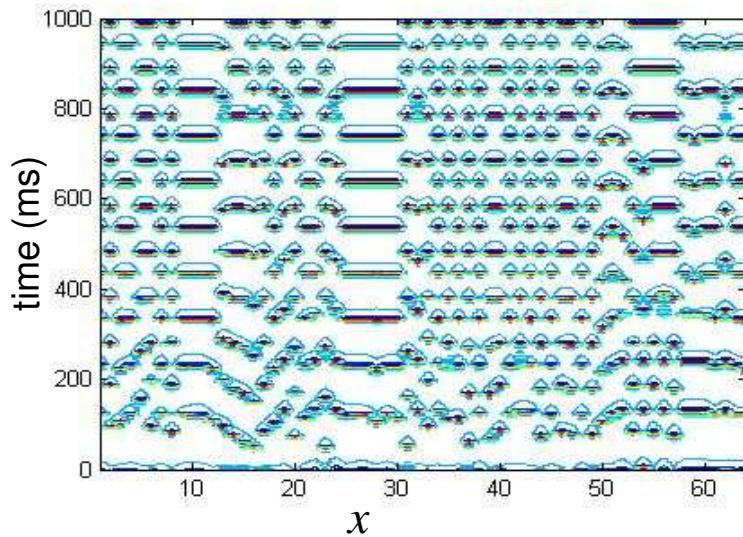
$c=0; N=0.01$





2. Multiscale connectivity in a neural model

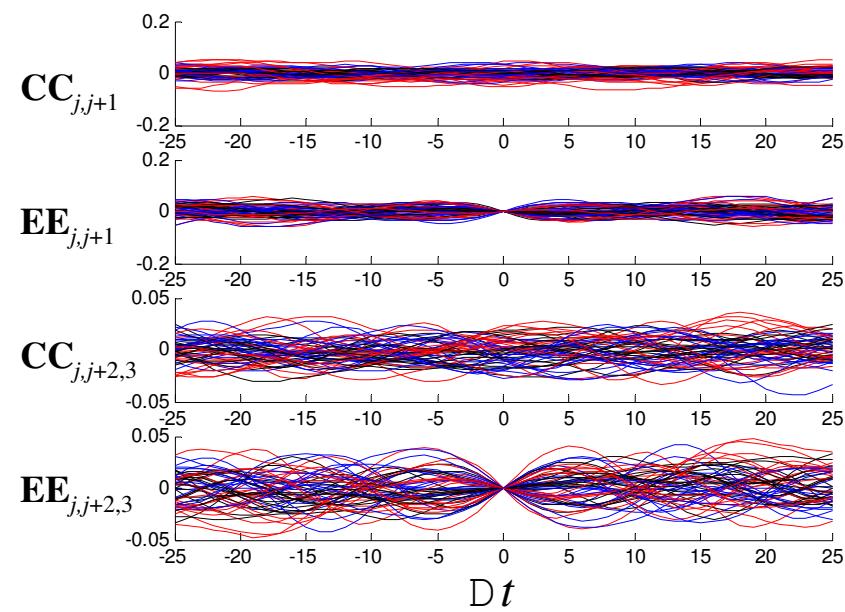
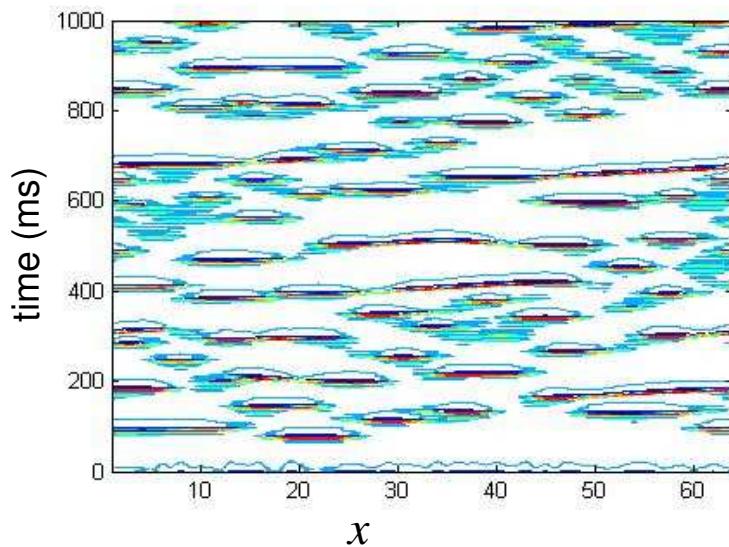
$$c=0.03; N=0.01$$





2. Multiscale connectivity in a neural model

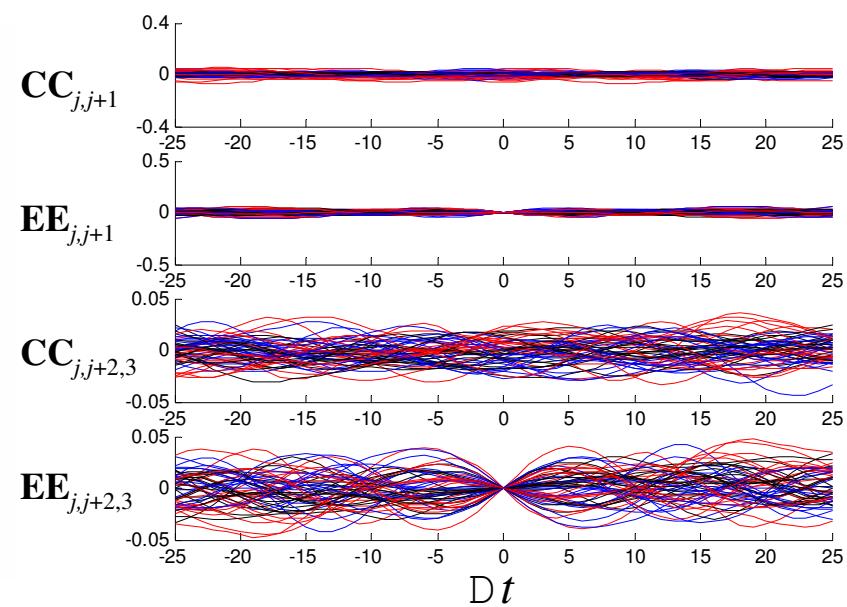
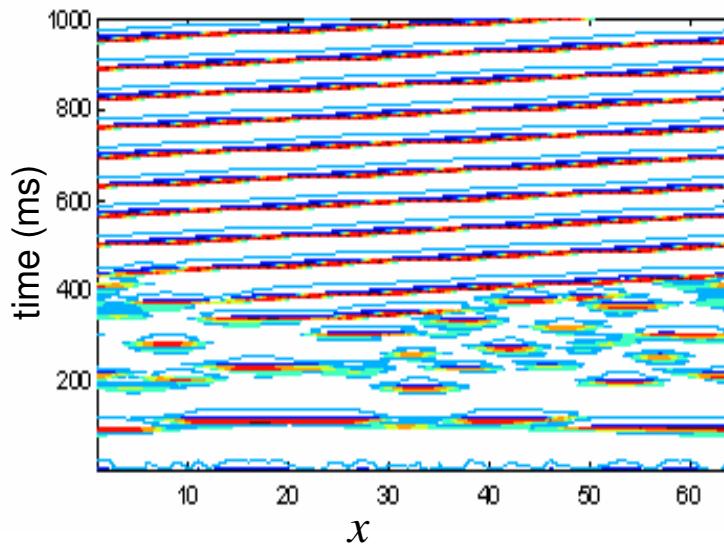
$c=3; N=16$





2. Multiscale connectivity in a neural model

$c=4; N=16$





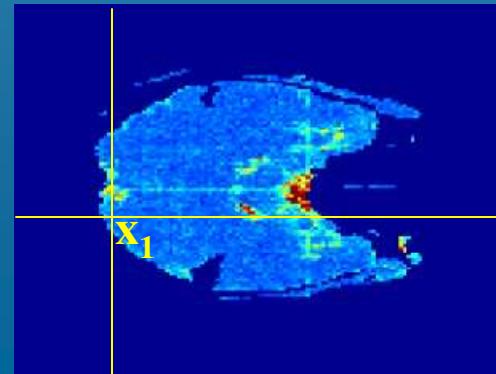
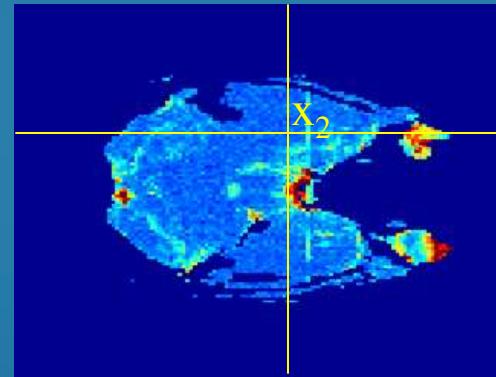
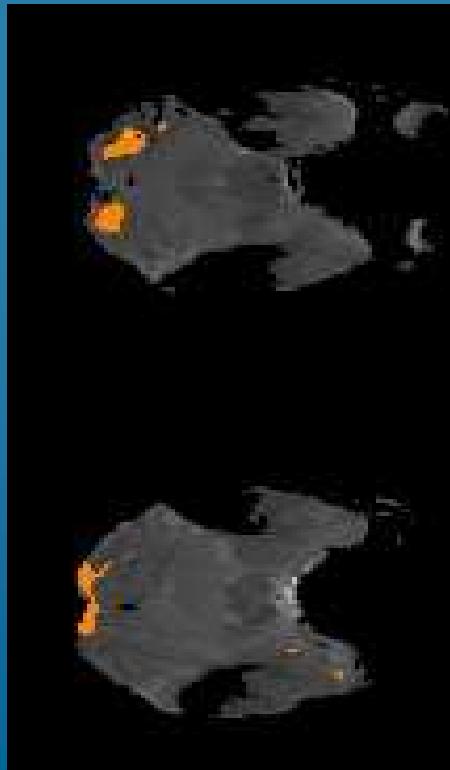
2. Multiscale connectivity in a fMRI data:

2.1 Two discrete regions

Within or between-scale correlations of fluctuations centred at two discrete points \mathbf{x}_1 and \mathbf{x}_2 can be defined as,

$$\text{CC}_{j_1, j_2}(\mathbf{x}_1, \mathbf{x}_2, \Delta t) = \frac{(d_{j_1}(\mathbf{x}_1, t), d_{j_2}(\mathbf{x}_2, t + \Delta t))_T}{\sqrt{(d_{j_1}(\mathbf{x}_1, t), B_{j_1}(\mathbf{x}_1, t))_T (d_{j_2}(\mathbf{x}_2, t + \Delta t), d_{j_2}(\mathbf{x}_2, t + \Delta t))_T}}$$

Note that $\text{CC}(\mathbf{x}_1, \mathbf{x}_2, 0)$ is not symmetric and hence does not permit the same decomposition (into **DD** and **EE**).





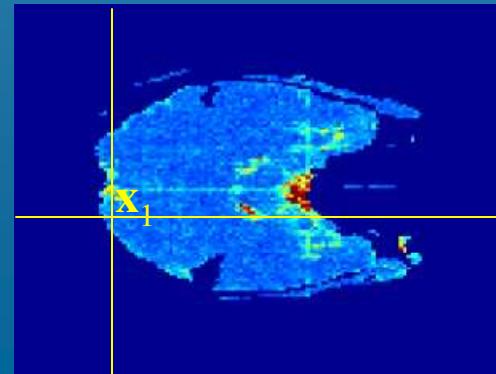
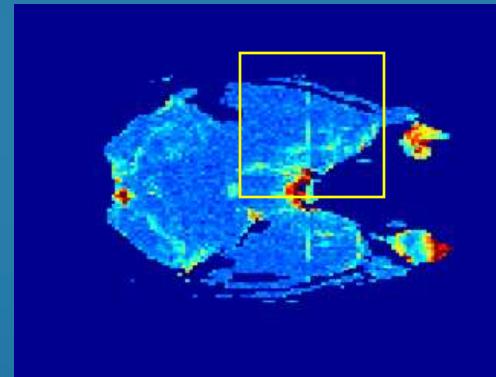
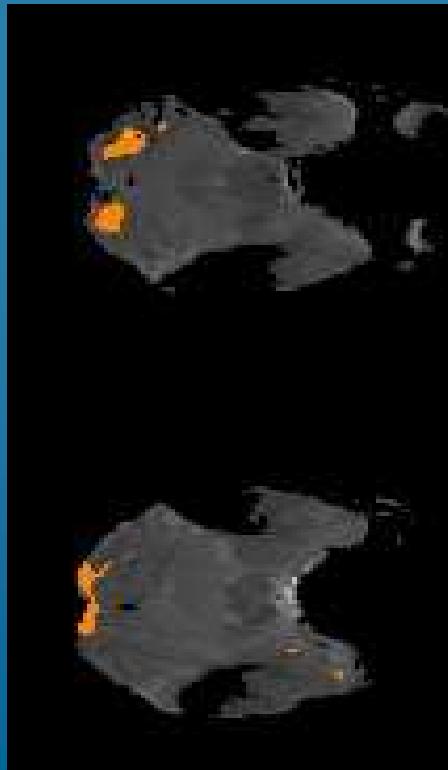
2. Multiscale connectivity in a fMRI data:

2.2 One discrete region and one brain network

Within or between-scale correlations of fluctuations between a discrete point \mathbf{x}_1 and a brain ‘domain’ Ω can be obtained by spatial integration,

$$\text{CC}_{j_1, j_2}(\mathbf{x}_1, \Omega, \Delta t) = \int_{\Omega} \text{CC}_{j_1, j_2}(\mathbf{x}_1, \mathbf{x}, \Delta t) d\mathbf{x}.$$

Again $\text{CC}(\mathbf{x}_1, \Omega, 0)$ is not symmetric and hence does not permit the same decomposition (into **DD** and **EE**).





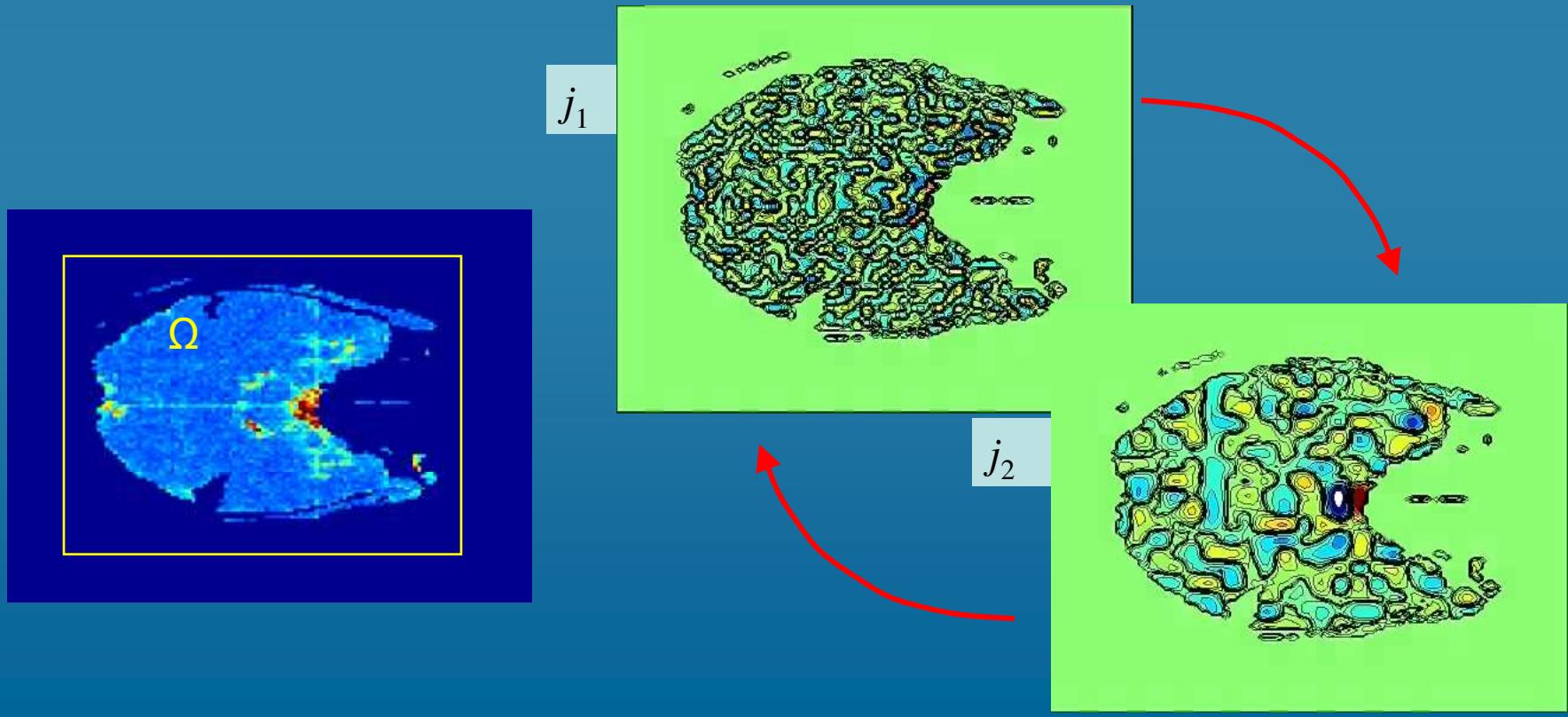
2. Multiscale connectivity in a fMRI data:

2.3 Within a brain network (between scales)

Between-scale correlations of fluctuations within a brain ‘domain’ Ω can be obtained by spatial integration,

$$\mathbf{CC}_{j_1, j_2}(\Omega, \Delta t) = \int_{\Omega} \mathbf{CC}_{j_1, j_2}(\mathbf{x}, \mathbf{x}, \Delta t) d\mathbf{x}.$$

Here $\mathbf{CC}(\Omega, 0)$ is symmetric and hence does permit a decomposition (into **DD** and **EE**).



3. Multiscale neurovascular coupling

As with the neuropil, the vasculature of the brain also exhibits a multiscale architecture (major and minor arteries, arterioles, capillaries, venules, etc.)

The BOLD signal Y contains signal from all such vessels ,

$$Y(\mathbf{x}, t) = \sum_j A_j y_j(\mathbf{x}, t),$$

where A_j is the contribution of signal y_j at scale j to Y .

We permit scale-specific neuro-vascular coupling and blood flow parameters as,

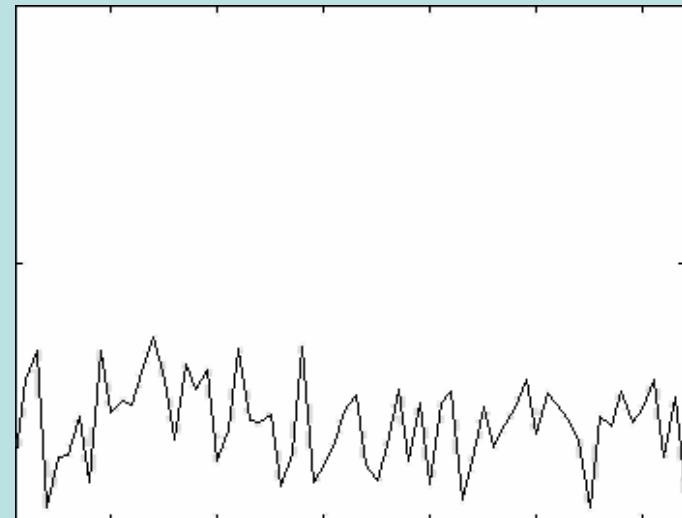
$$y_j(\mathbf{x}, t) = \iint_{\Omega} M_j(\Lambda^j V(\mathbf{x}, t - \tau)) \otimes h_j(t) dt \otimes S(\mathbf{x}') d\mathbf{x}$$

where

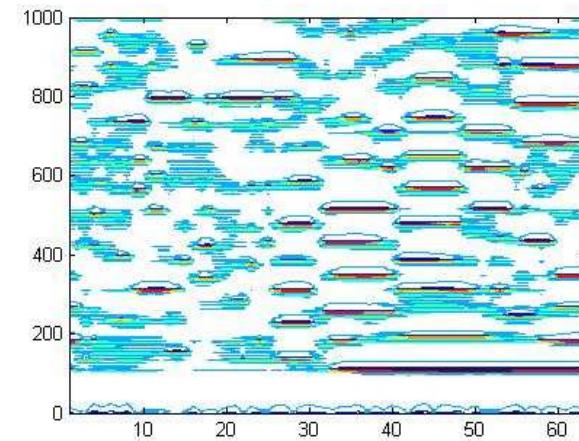
$$M(V(\mathbf{x}, t)) = \left| \frac{dV(\mathbf{x}, t)}{dt} \right|, \quad \text{is the metabolic demand function}$$

3. Multiscale neurovascular coupling

$V(x, t)$
(neural activity)

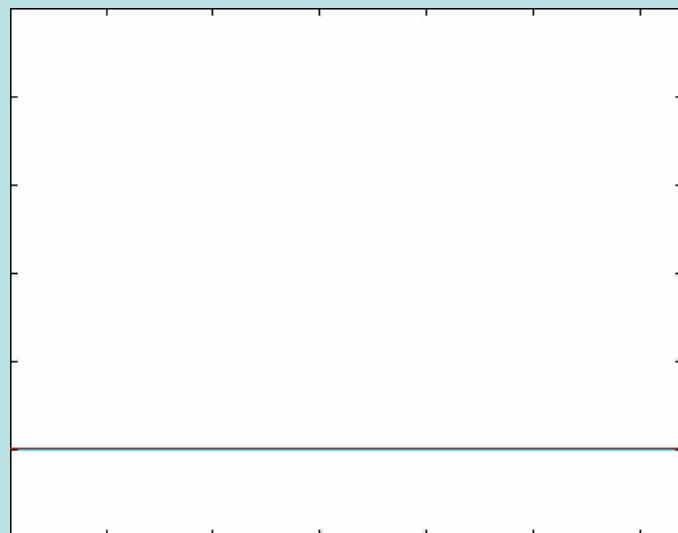


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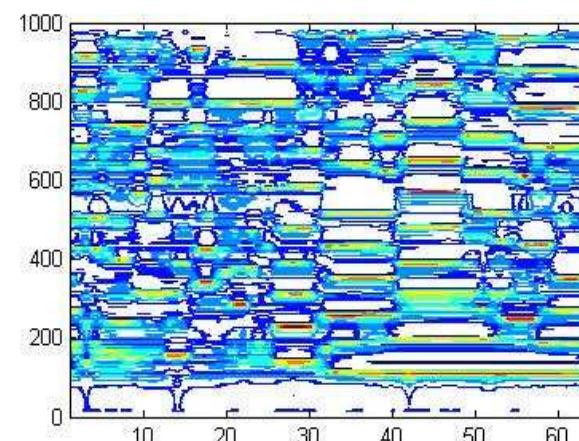


$$Y(x, t) = \int \int_{\Omega \tau} M(V(x, t - \tau)) \otimes h(t) dt \otimes S(x') dx$$

$Y(x, t)$
(BOLD)

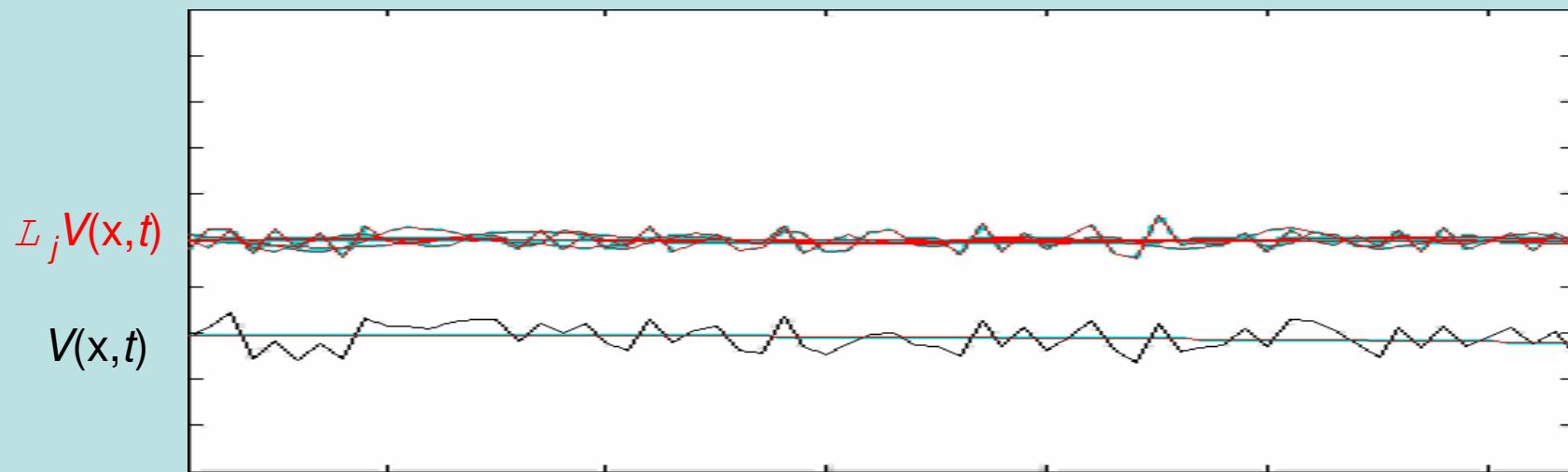


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Buxton & Frank (1997), Friston *et al.* (2000)

3. Multiscale neurovascular coupling



$$y_j(\mathbf{x}, t) = \int \int_{\Omega \tau} M_j(\Lambda^j V(\mathbf{x}, t - \tau)) \otimes h_j(t) dt \otimes S(\mathbf{x}') d\mathbf{x}$$

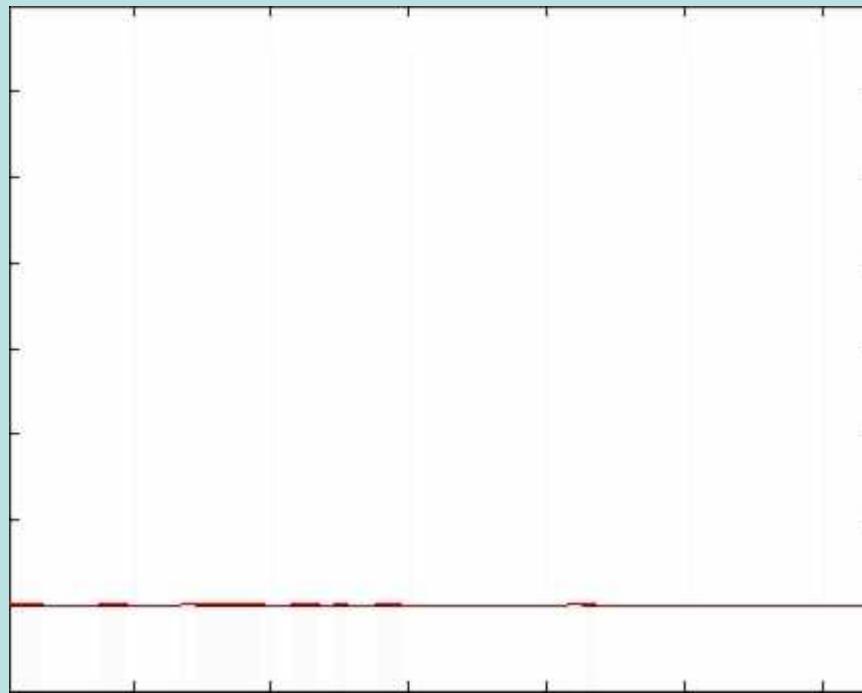
$Y(\mathbf{x}, t)$
 $y_j(\mathbf{x}, t)$



3. Multiscale neurovascular coupling

$$Y^w(\mathbf{x}, t) = \sum_j A_j y_j(\mathbf{x}, t),$$

$$Y(\mathbf{x}, t)$$



$$A_j = 1,$$

$$\tau_j = 1.3.$$

3. Multiscale neurovascular coupling

$$Y^w(\mathbf{x}, t) = \sum_j A_j y_j(\mathbf{x}, t),$$

$$Y(\mathbf{x}, t)$$

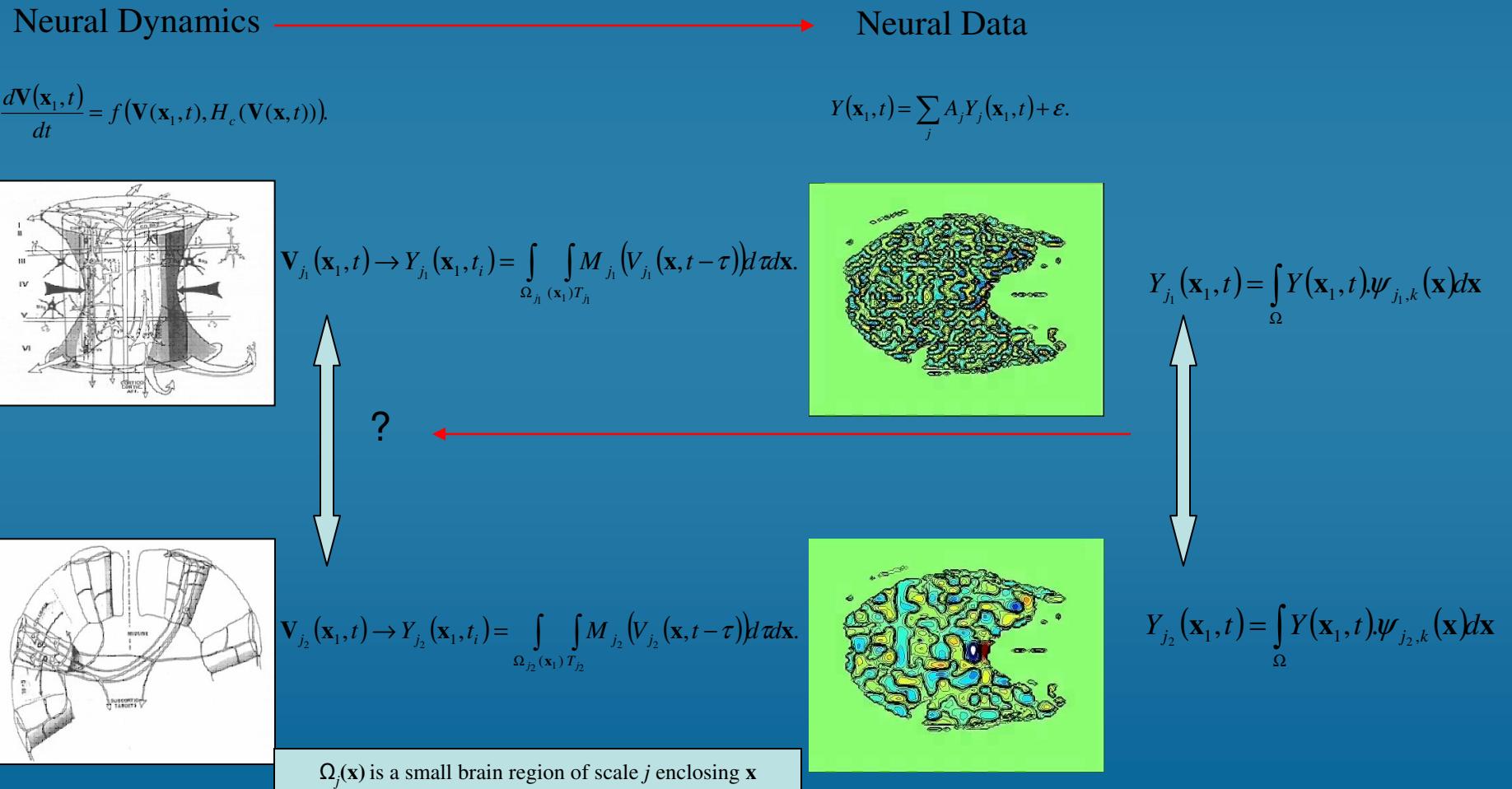


$$A_1 = [4 \quad 2.5 \quad 2 \quad 1 \quad 1 \quad 1 \quad 1],$$

$$\tau_j = 1.3^j.$$

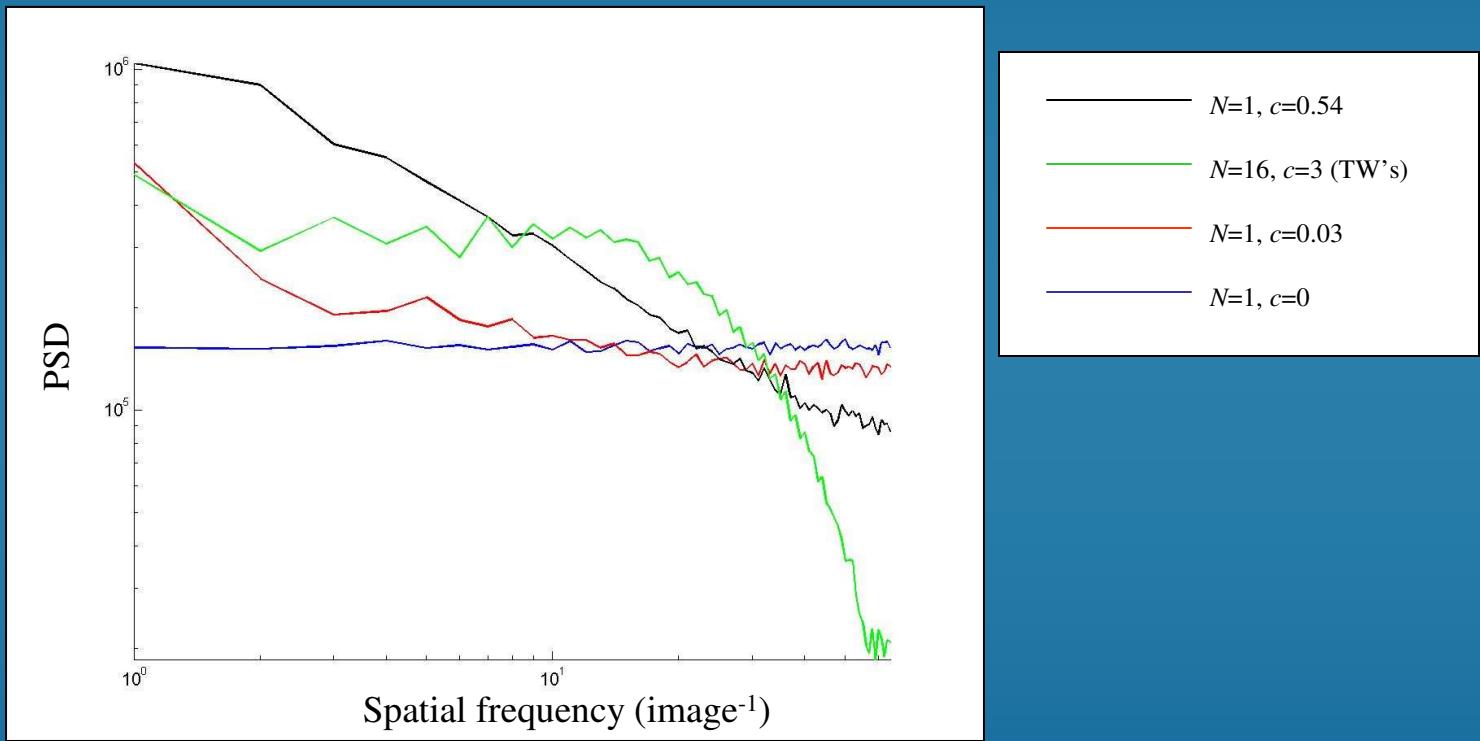
3. Multiscale neurovascular coupling

As with functional connectivity, multiscale connectivity does not directly reflect neural effects



5. General multiscale brain theory

Coupling causes scale-free and scale-specific emergent phenomena in the spatial domain:

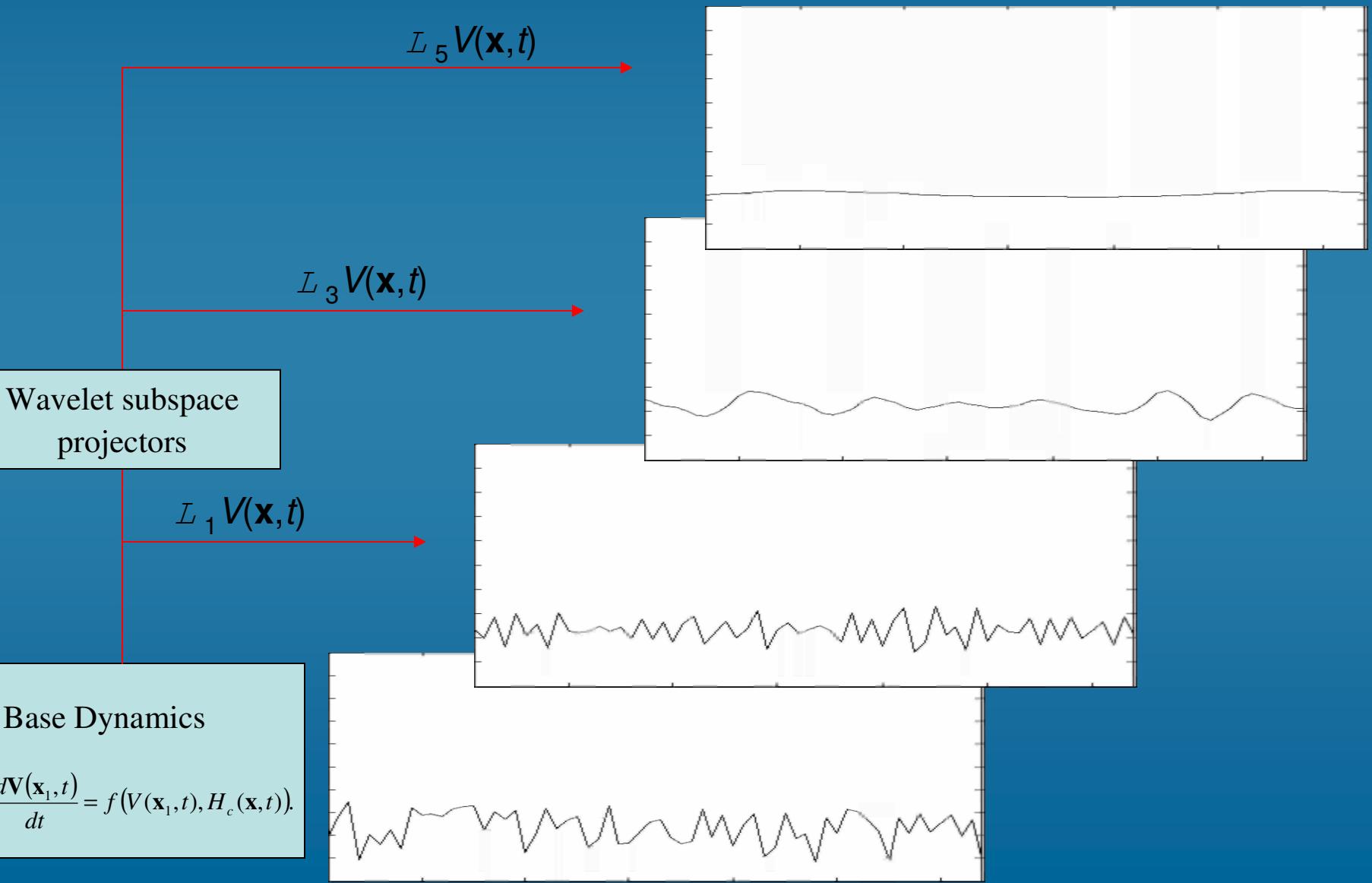


Unlike many ‘scale-free’ physical systems, the brain has an *a priori* (multiscale) architecture from which such scale-free dynamics emerge

How to model scale-free dynamical systems interacting within a multiscale architecture?

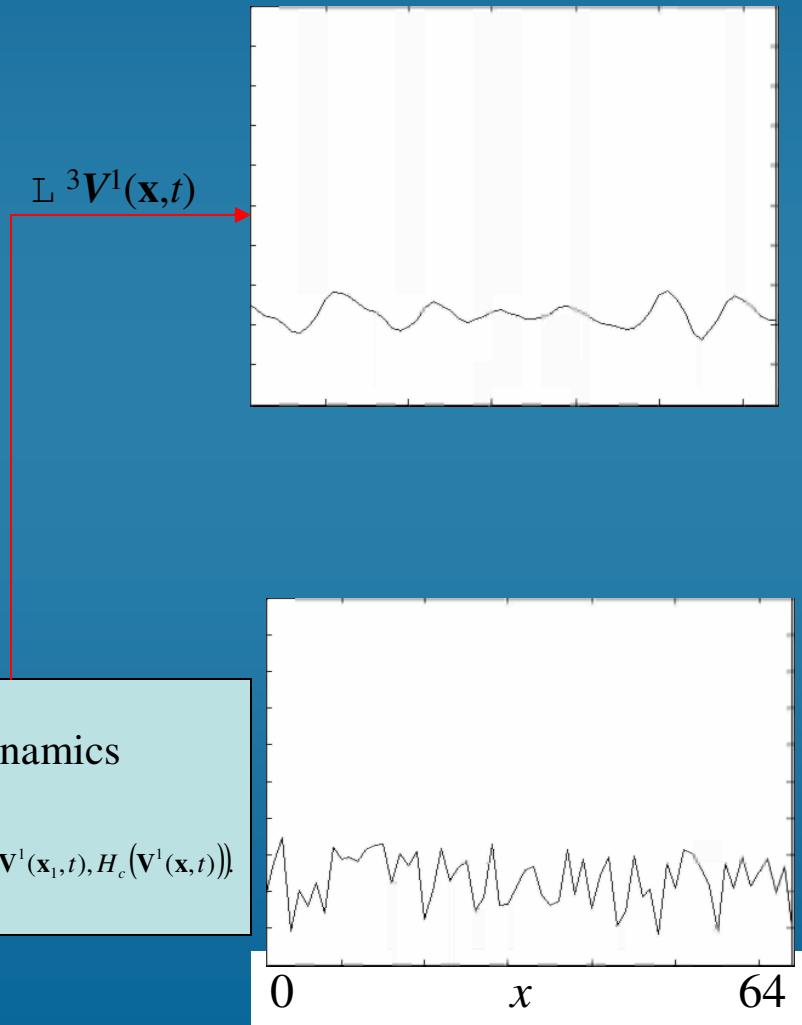
Multiscale Neural Modelling

Emergent phenomena are reflected in the wavelet subspace projections



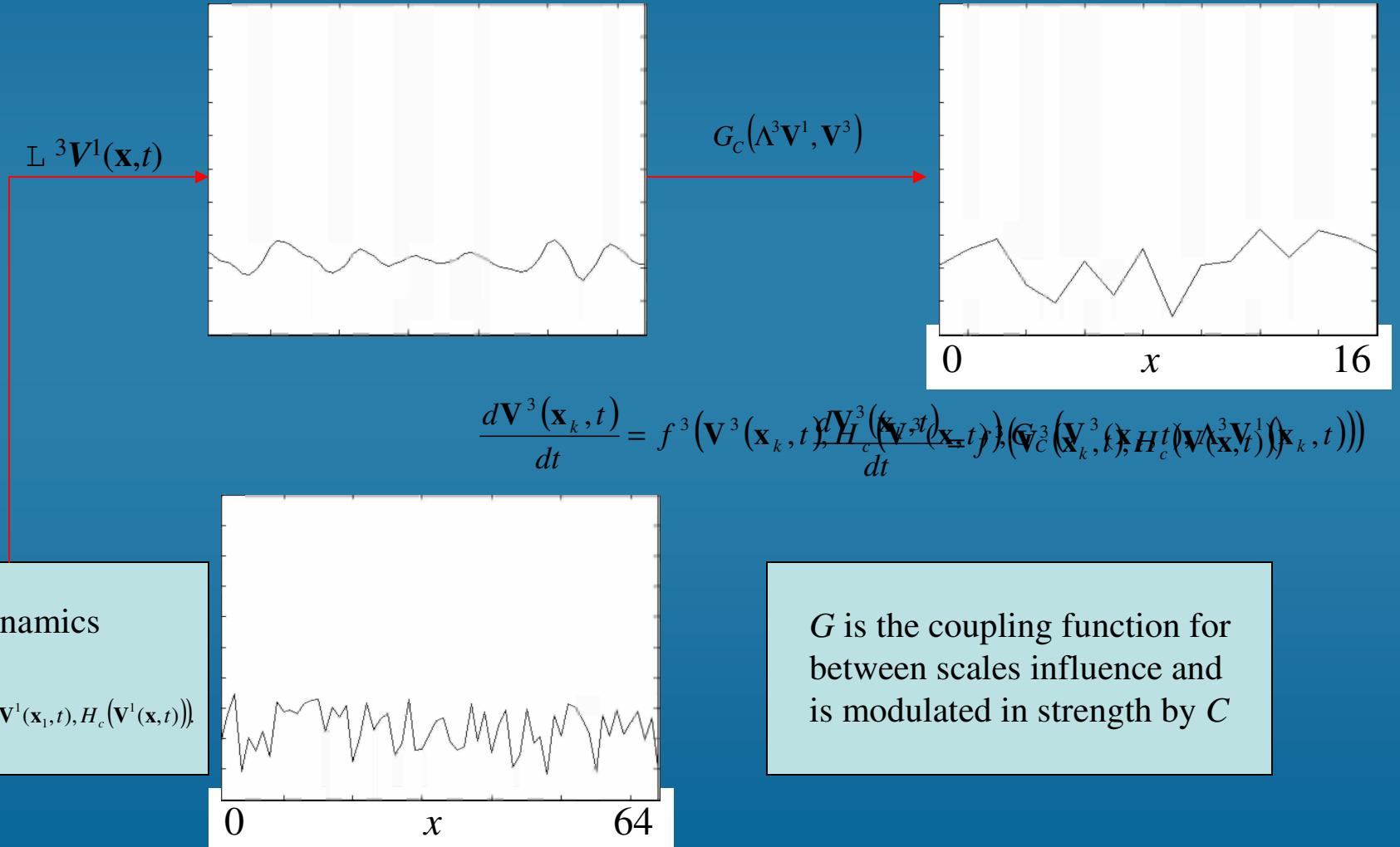
Multiscale Neural Modelling

Why not add larger scale systems and use the scale-congruent projections to drive them?



Multiscale Neural Modelling

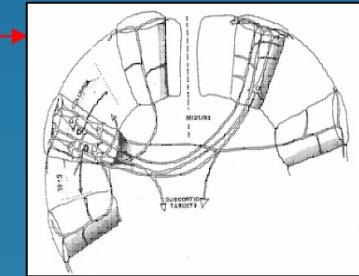
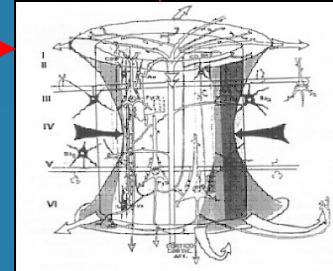
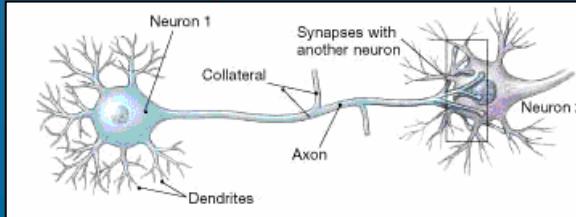
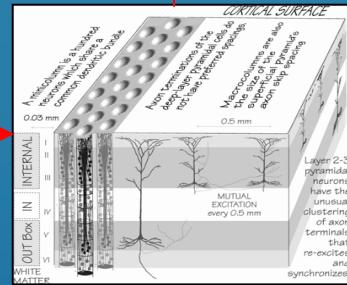
Why not add larger scale systems and use the scale-congruent projections to drive them?



Multiscale Neural Modelling

Recursive application of subspace projection and coupling enables construction of a dynamic multiscale hierarchy

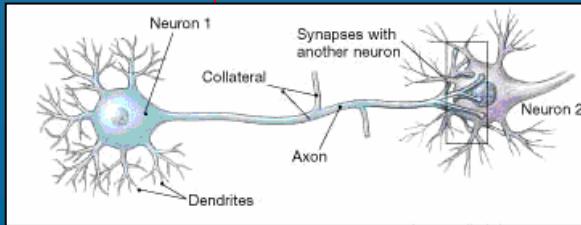
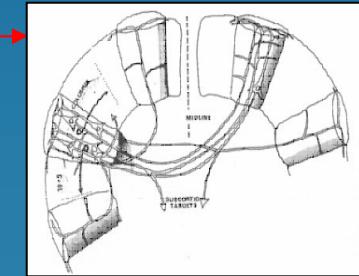
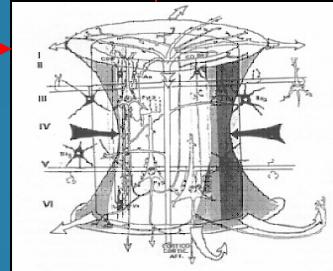
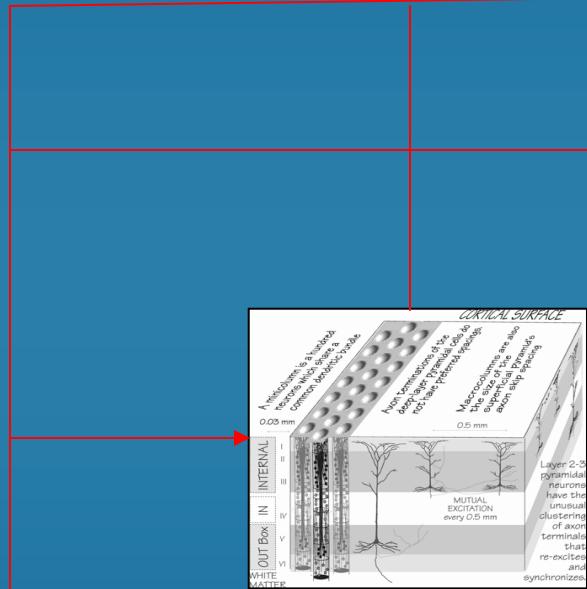
Wavelet subspace
projectors



$$\begin{aligned}\frac{d\mathbf{V}^j(\mathbf{x}_k, t)}{dt} &= f^j \left(\mathbf{V}^j(\mathbf{x}_k, t), H_{c_j}(\mathbf{V}^j(\mathbf{x}, t)), \sum_{i < j} G_{C_{i,j}}(\mathbf{V}^j(\mathbf{x}_k, t), W^j \mathbf{V}^i(\mathbf{x}_k, t)) \right) \\ &= f^j(\mathbf{V}^j(\mathbf{x}_k, t)) + H_{e_j}(\mathbf{V}^j(\mathbf{x}, t)) + \sum_{i < j} G_{C_{i,j}}(\mathbf{V}^j(\mathbf{x}_k, t), W^{ij} \mathbf{V}^i(\mathbf{x}_k, t)).\end{aligned}$$

Multiscale Neural Modelling

Addition of a time-scale multiplier also permits geometric temporal multiscale nesting (following Fujimoto & Kaneko *Physica D* **180**: 1-16.)

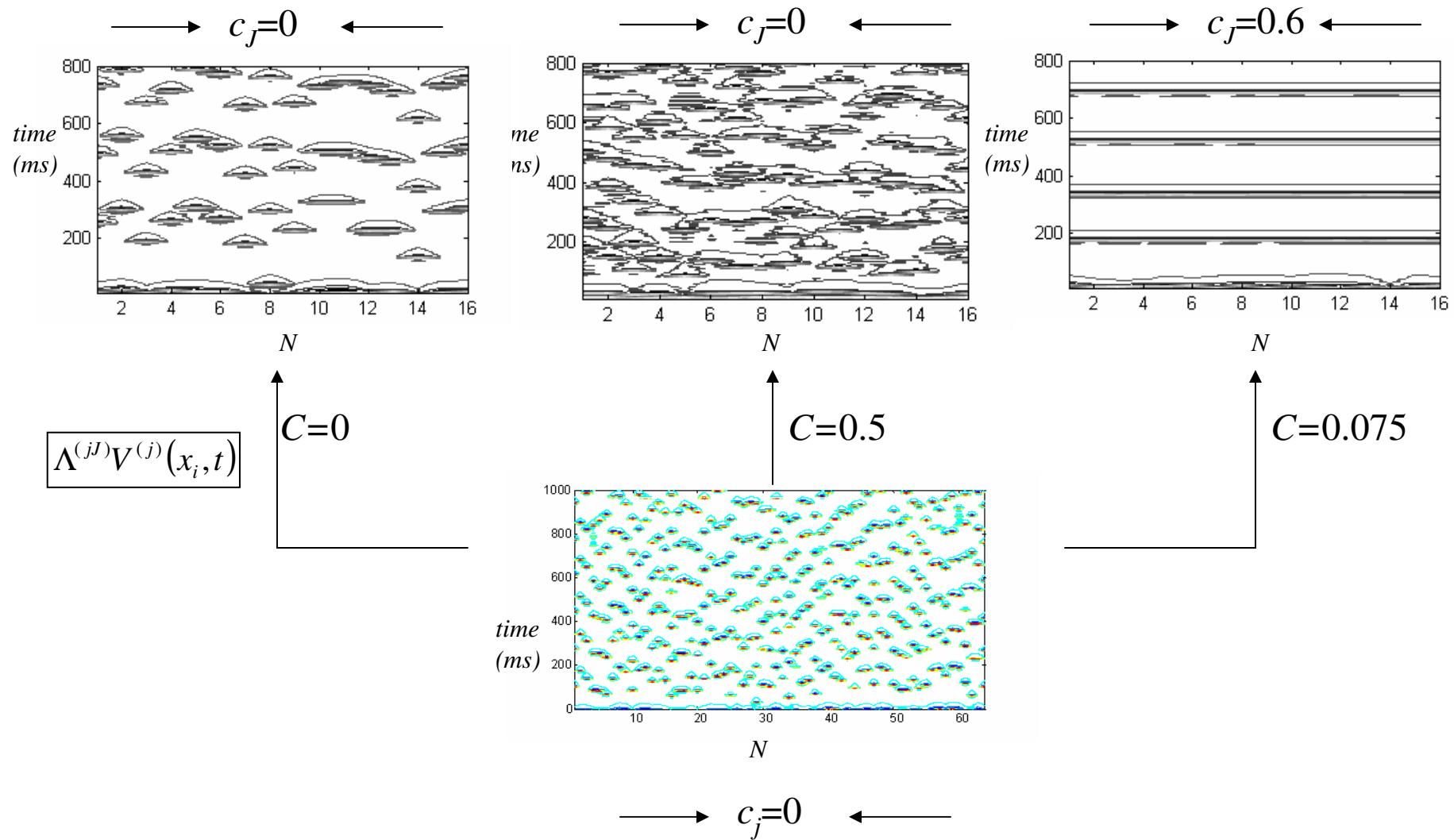


$$T^j \frac{d\mathbf{V}^j(\mathbf{x}_k, t)}{dt} = f^j \left(\mathbf{V}^j(\mathbf{x}_k, t), H_{c_j}(\mathbf{V}^j(\mathbf{x}, t)), \sum_{i < j} G_{C_{i,j}}(\mathbf{V}^j(\mathbf{x}_k, t), W^j \mathbf{V}^i(\mathbf{x}_k, t)) \right)$$

$T < 1$ ensures the smallest spatial scales have the fastest time scales

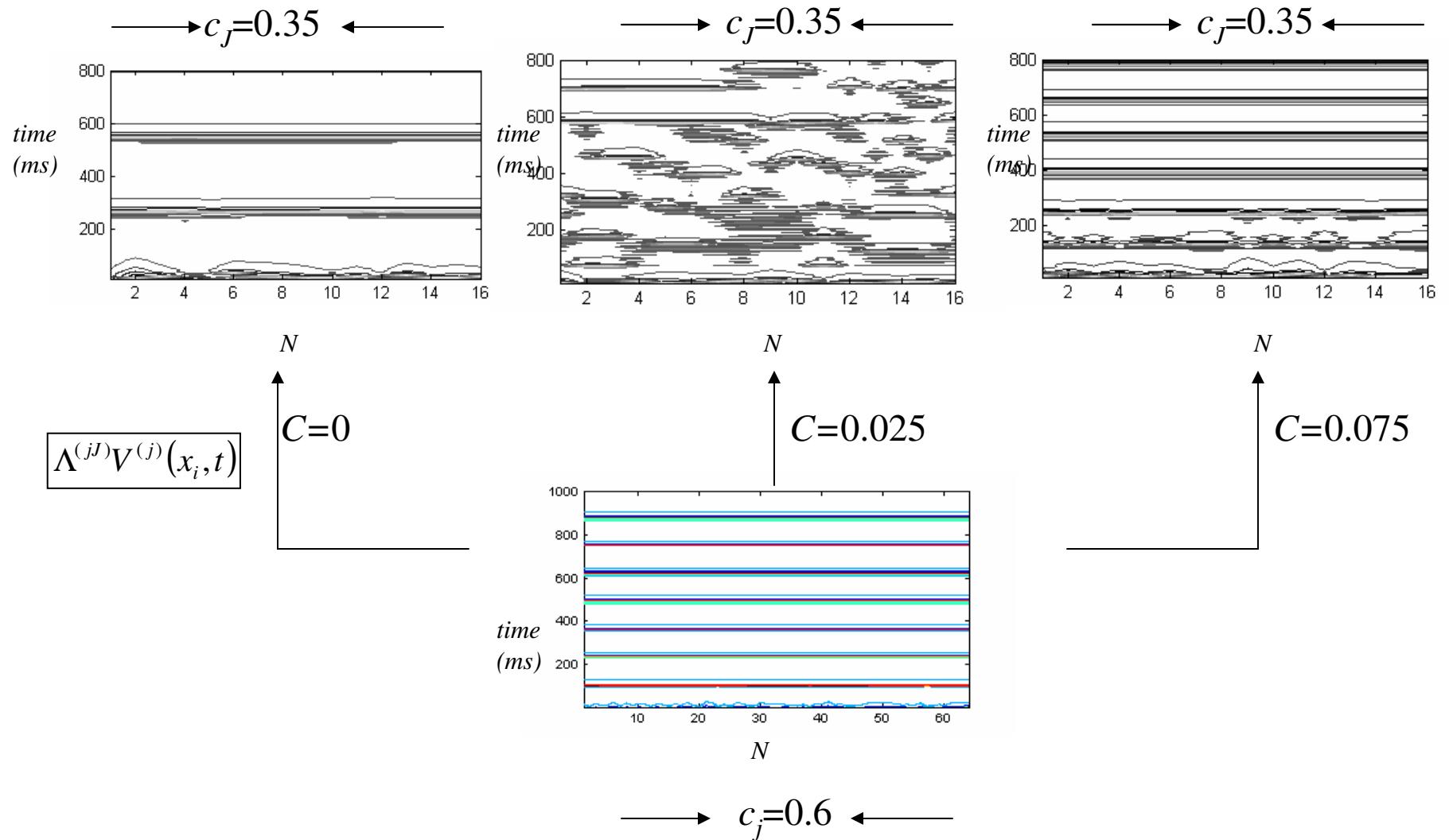
Multiscale Neural Modelling

Uncoupled fine grained system, $c_j=0$ and $T=1$.



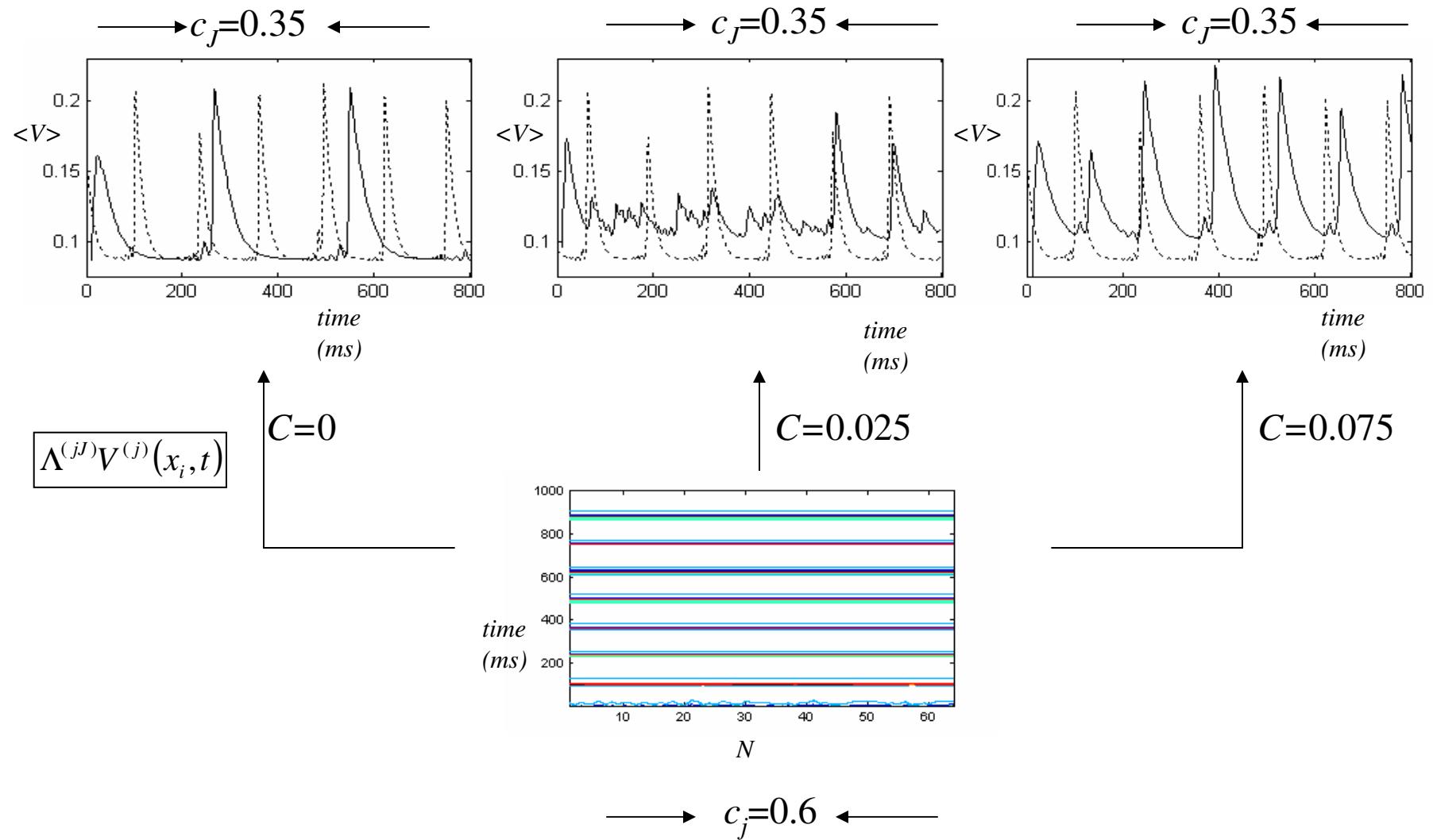
Multiscale Neural Modelling

Synchronized fine grained system, $c_j=0.6$ and $T=2$.



Multiscale Neural Modelling

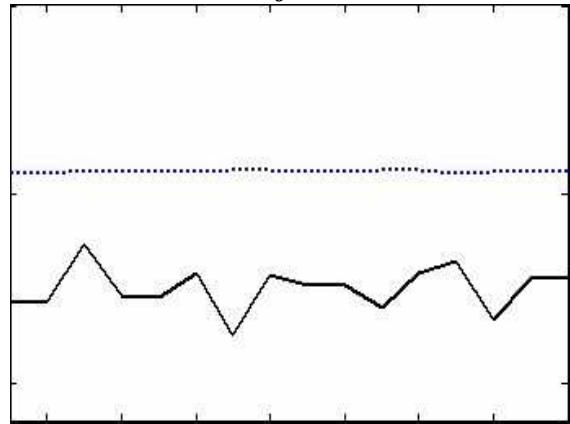
Synchronized fine grained system, $c_j=0.6$ and $T=2$.



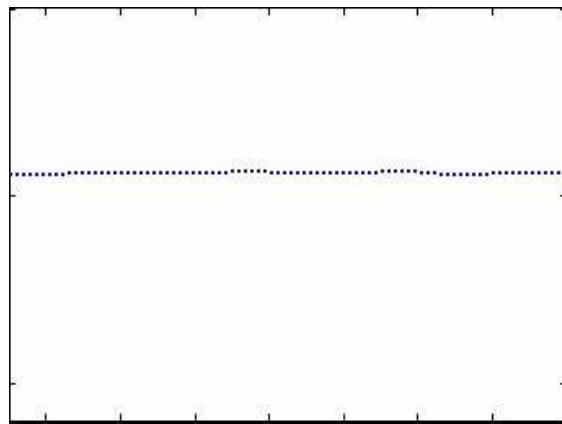
Multiscale Neural Modelling

Fine grained travelling waves, $c_j=0.54$ and $T=1$.

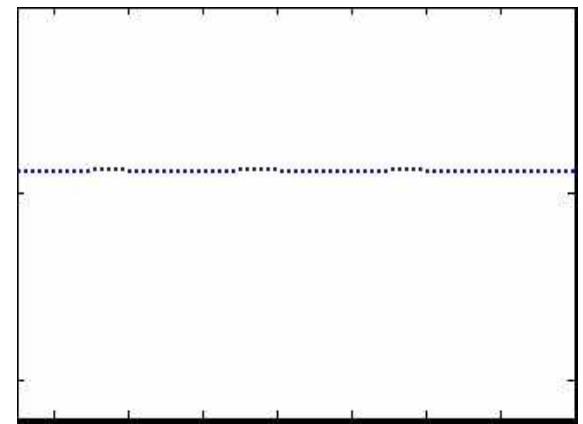
$$\longrightarrow c_j=0.1 \longleftarrow$$



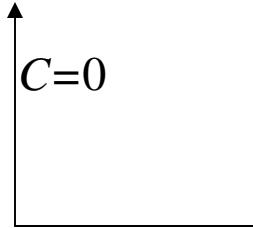
$$\longrightarrow c_j=0.05 \longleftarrow$$



$$\longrightarrow c_j=0.6 \longleftarrow$$

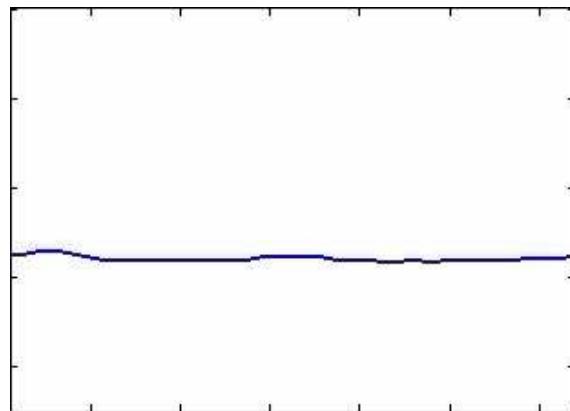


$$\boxed{\Lambda^{(j)} V^{(j)}(x_i, t)}$$



$$N$$

 $C=0.4$

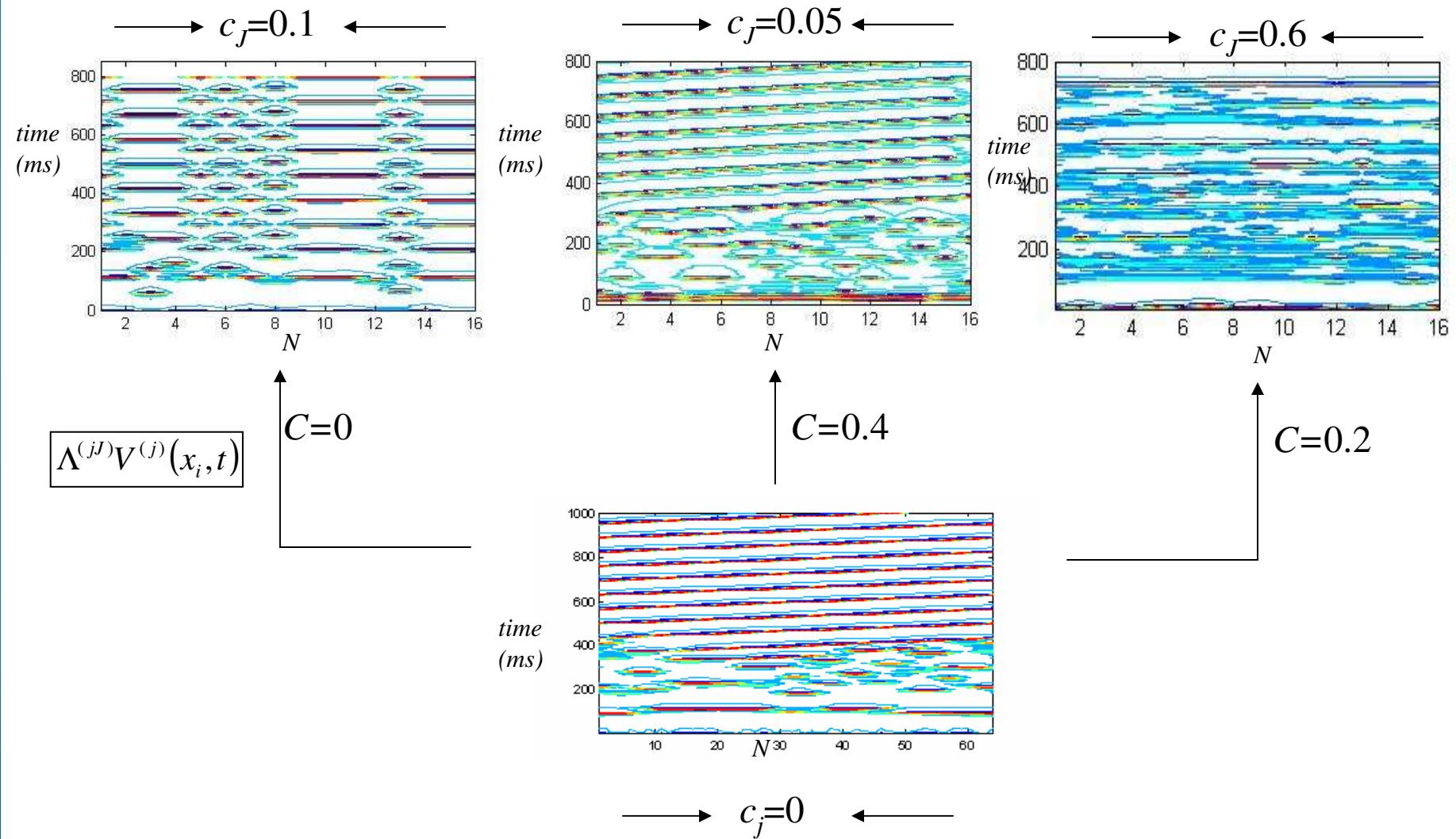


$$N$$

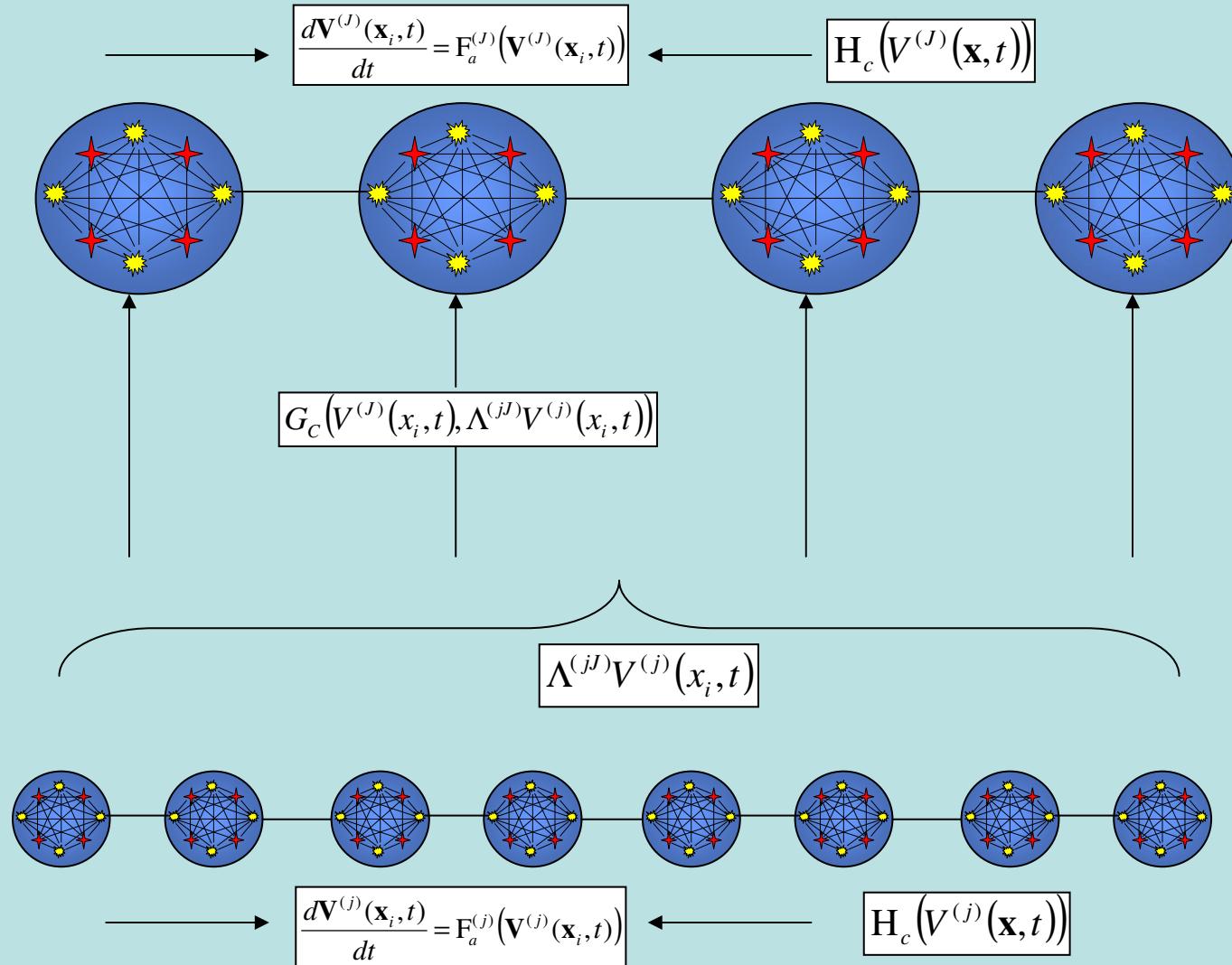
 $C=0.2$

Multiscale Neural Modelling

Fine grained travelling waves, $c_j=0.54$ and $T=1$.

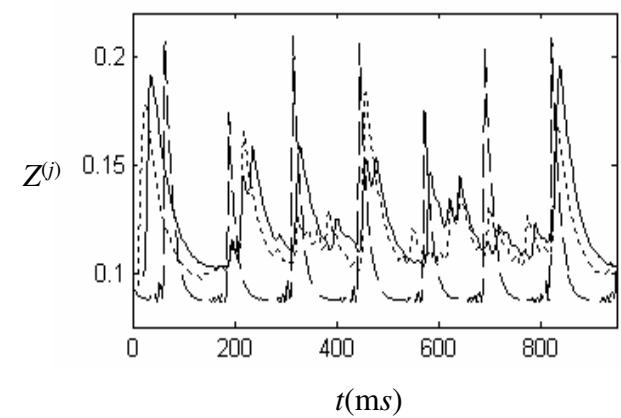
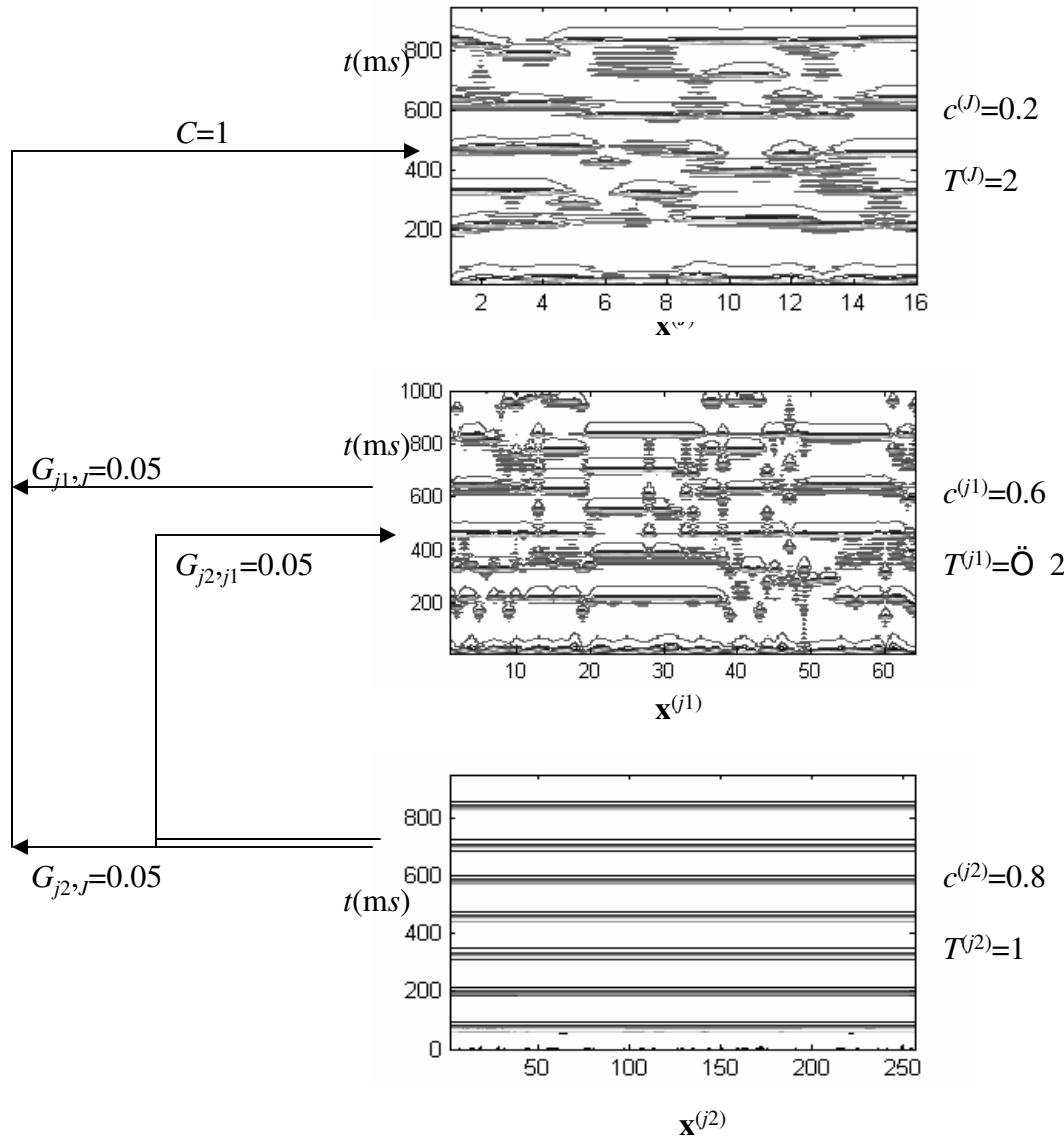


Multiscale Neural Modelling

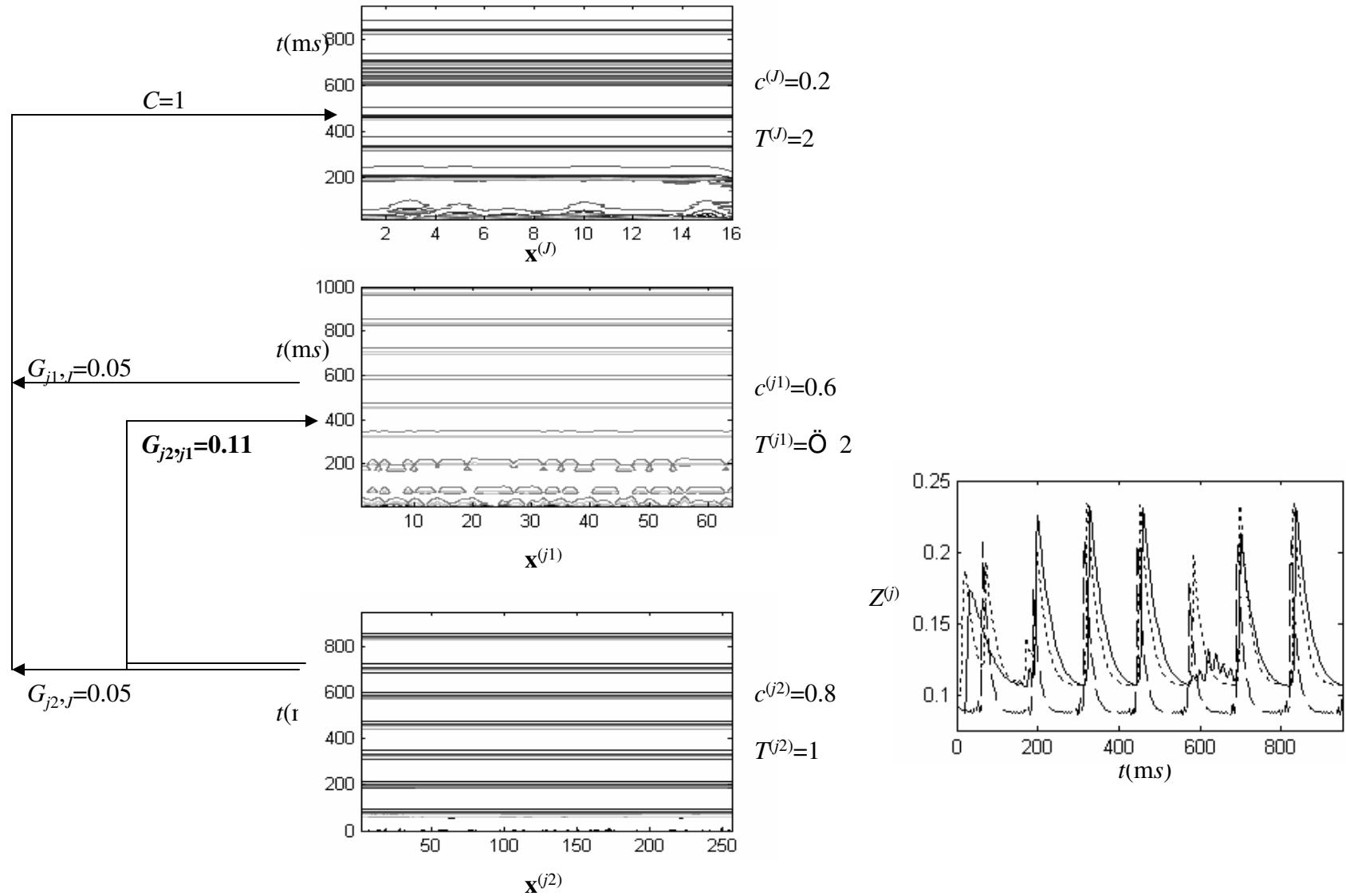


Breakspear & Stam. (2005) *Phil. Trans. Royal Soc. Lon. B*

Three tiered system



Three tiered system



5. General multiscale brain theory

Hence, a multiscale neural evolution equation:

$$\frac{d\mathbf{V}^{(J)}(\mathbf{x}_i, t)}{dt} = \mathbf{F}_{\mathbf{a}}^{(J)} \left(\mathbf{V}^{(J)}(\mathbf{x}_i, t) + c \sum_k H_{ik} \mathbf{V}^{(J)}(\mathbf{x}_k, t) + C \sum_{j < J} G_{jJ} \left(\Lambda^{(J)} \mathbf{V}^{(j)}(\mathbf{x}_i, t) + \overline{\mathbf{V}^{(j)}(\mathbf{x}, t)} - \mathbf{V}^{(J)}(\mathbf{x}_i, t) \right) \right)$$

and a scale-specific projections of neural data into measurement space,

$$Y(\mathbf{x}, t) = \sum_j \int \int M_j (\Lambda^j V(\mathbf{x}, t - \tau)) \otimes h_j(t) dt \otimes S(\mathbf{x}') d\mathbf{x}$$