Network *Meso*-Dynamics

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Outline or Why ? What ? How ?

- *Why* look at mesoscopic level of networks ?

- *What* structures underlie real life networks ?

  R K Pan & SS, EPL (2009); R K Pan, N Chatterjee & SS, PLoS ONE (2010)

- *How* do such structures affect network dynamics ? (synchronization, spin ordering, etc)

  S Dasgupta, R K Pan & SS, PRE Rapid (2009); SS & S Poria, Pramana (2011)

- *Why* do such structures arise in nature ?

  R K Pan & SS, PRE Rapid (2007); N Pradhan, S Dasgupta & SS, EPL (2011)

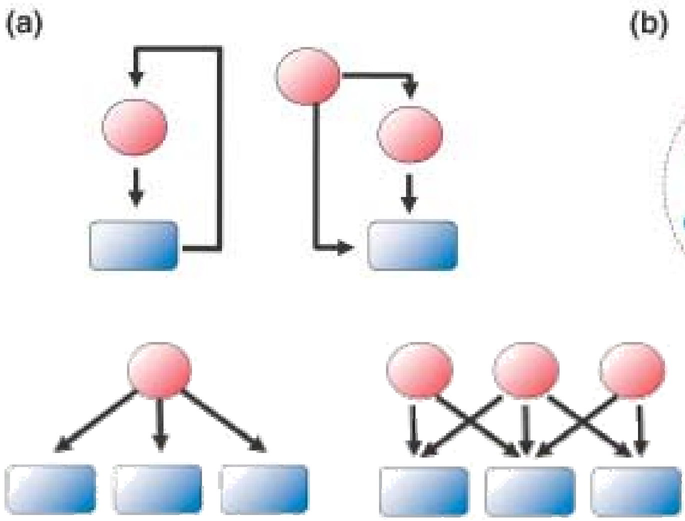
Significant for understanding coordination processes such as consensus formation & adoption of innovations

Modular Networks: dense connections *within* certain sub-networks (modules) & relatively few connections *between* modules

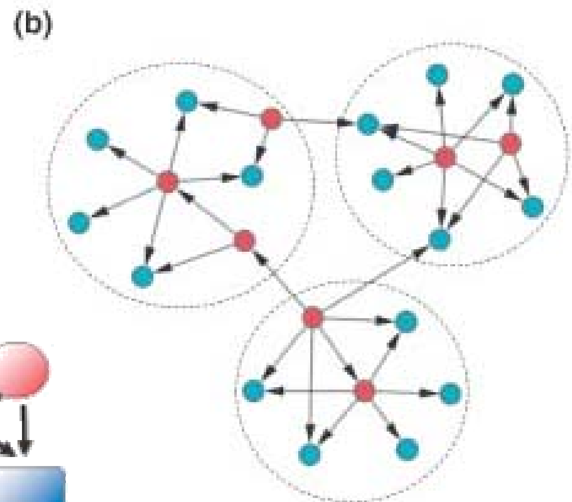
Modules: A *mesoscopic* organizational principle of networks

Going beyond ***motifs*** but more detailed than ***global*** description (L, C etc.)

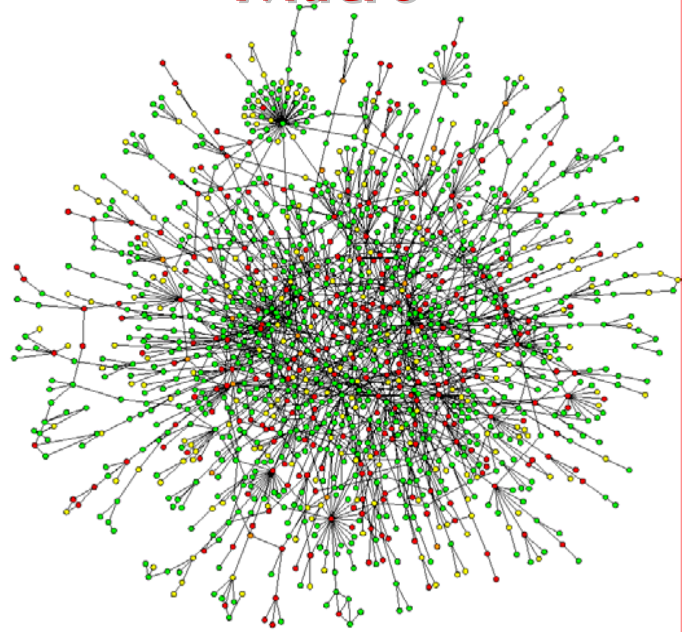
Micro



Meso



Macro



Kim & Park, WIREs Syst Biol & Med, 2010

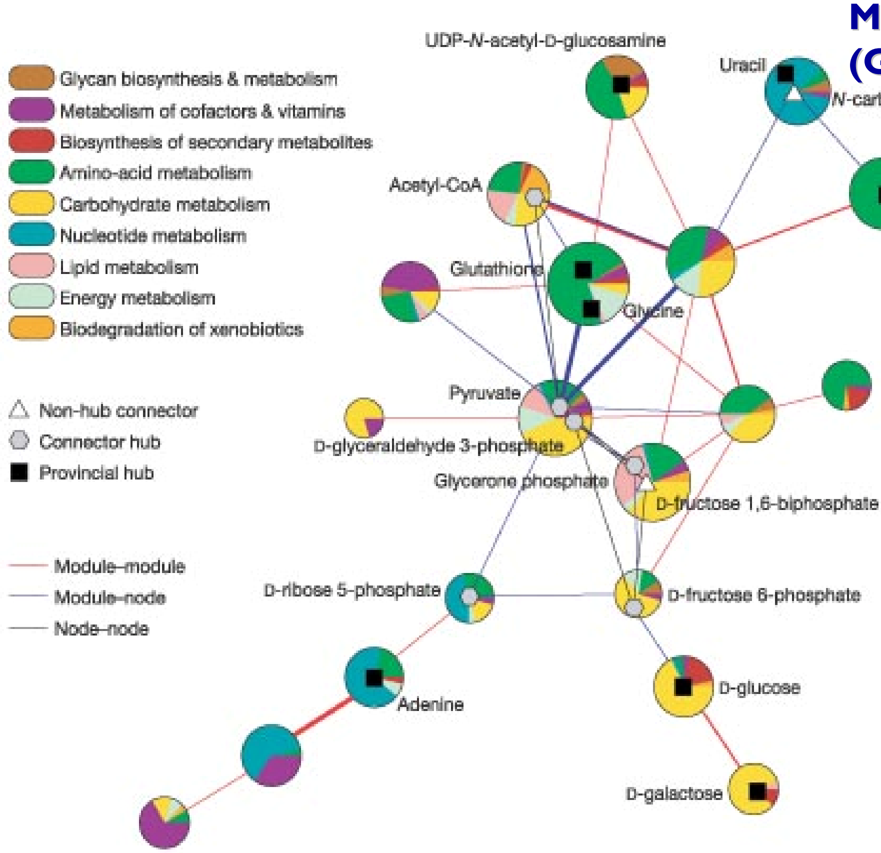
Ubiquity of modular networks

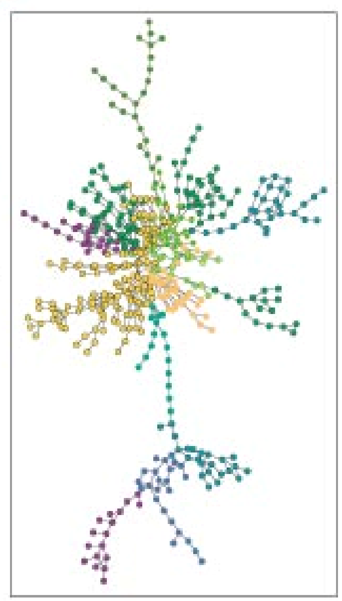
Modular Biology (Hartwell et al, Nature 1999)

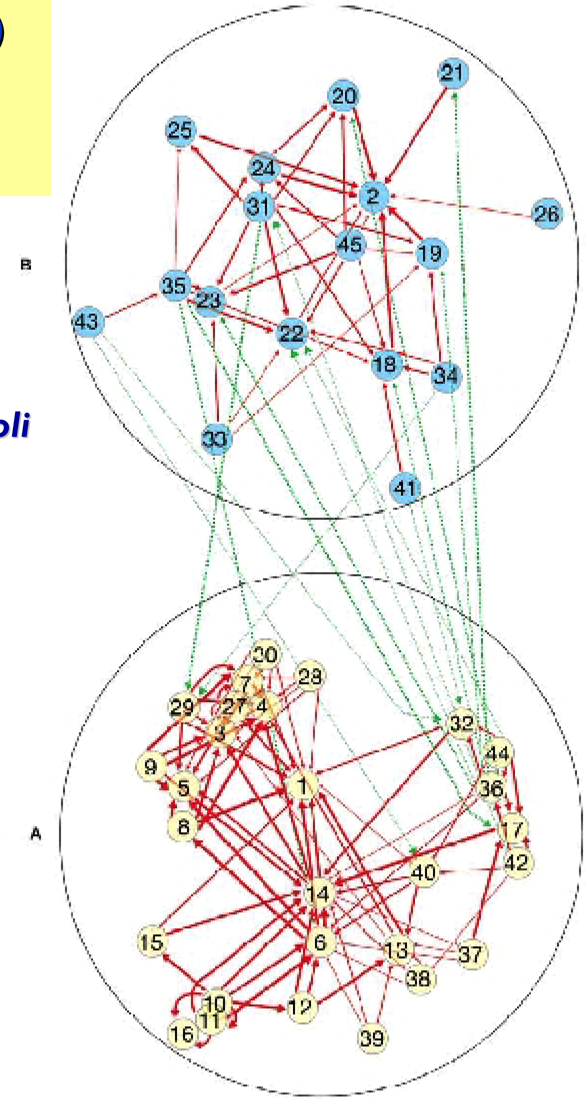
Functional modules as a critical level of biological organization

Modules in biological networks are often associated with specific functions

Metabolic network of *E coli* (Guimera & Amaral)

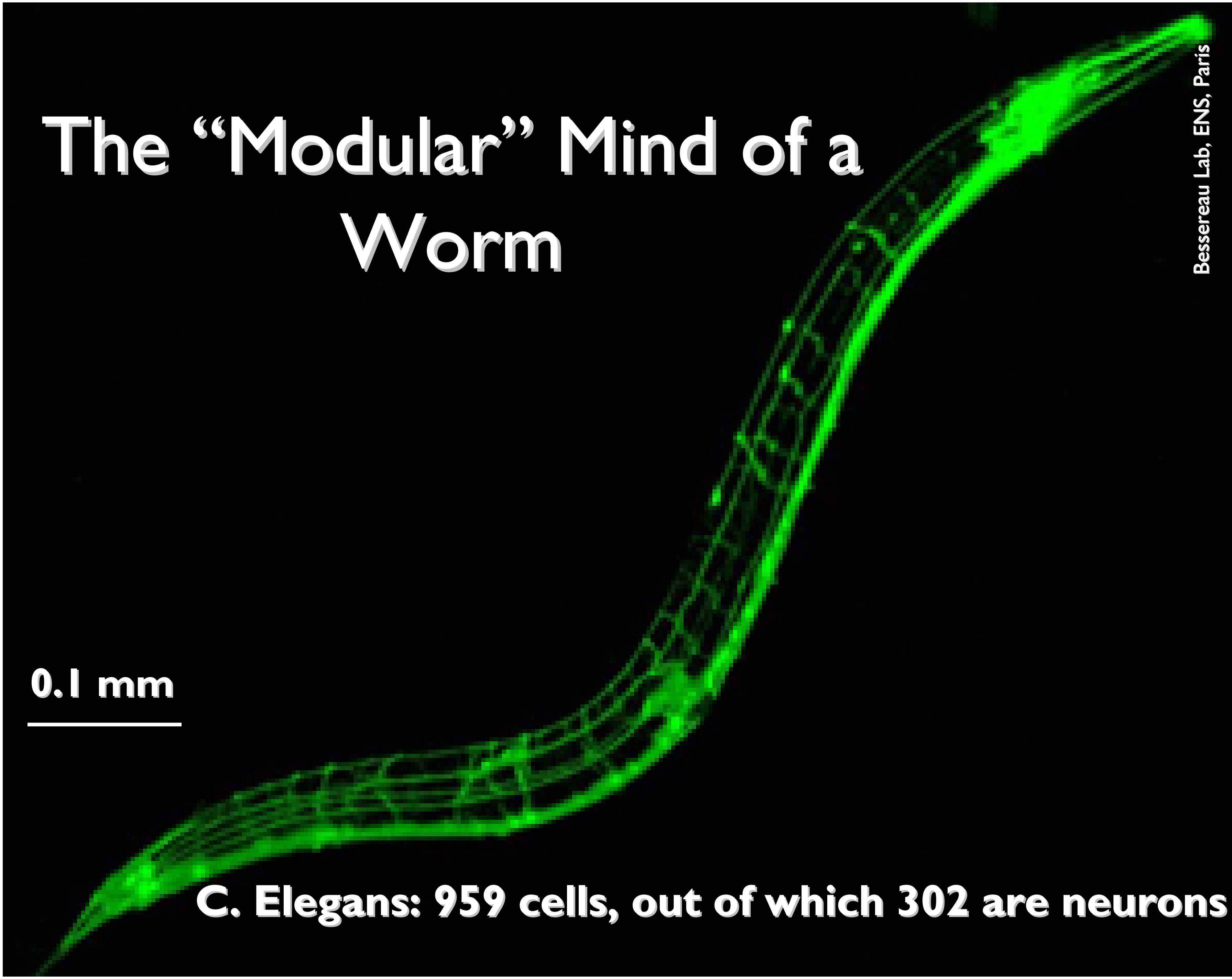






Chesapeake Bay foodweb (Ulanowicz et al)

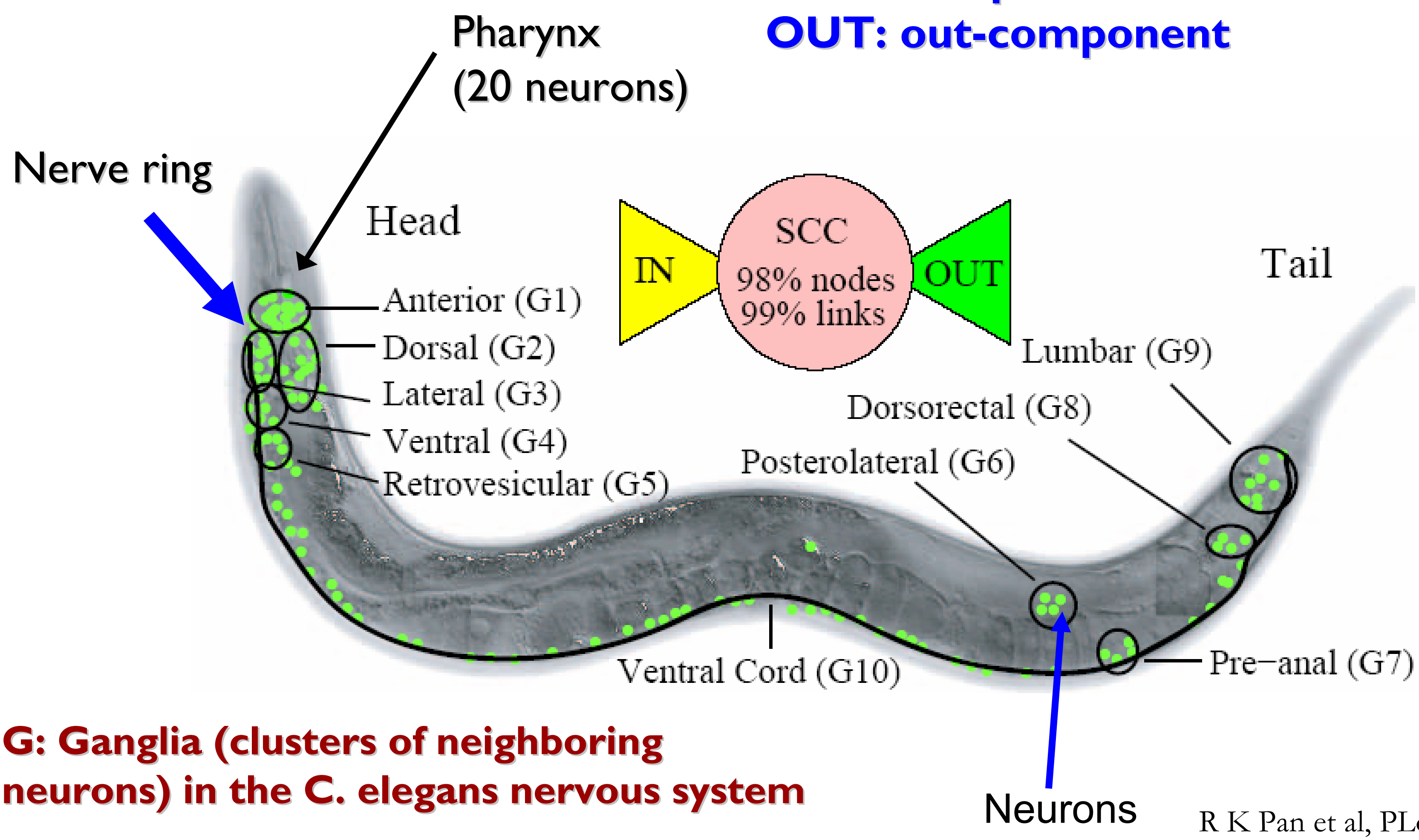
The “Modular” Mind of a Worm



Structure of the nervous system

Focus on the 282 non-pharyngeal neurons

SCC: strongly connected component
IN: in-component
OUT: out-component



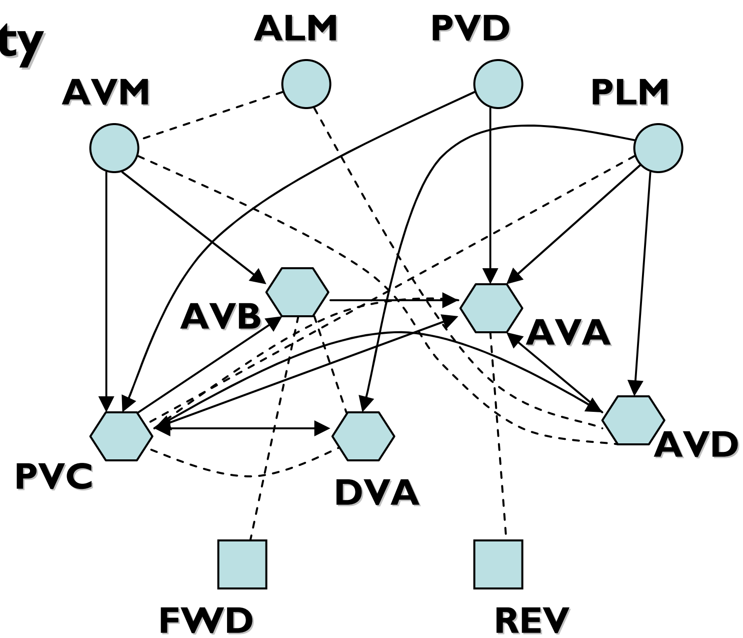
G: Ganglia (clusters of neighboring neurons) in the C. elegans nervous system

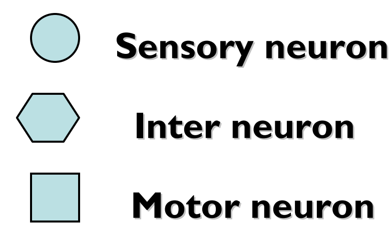
R K Pan et al, PLoS One (2010)

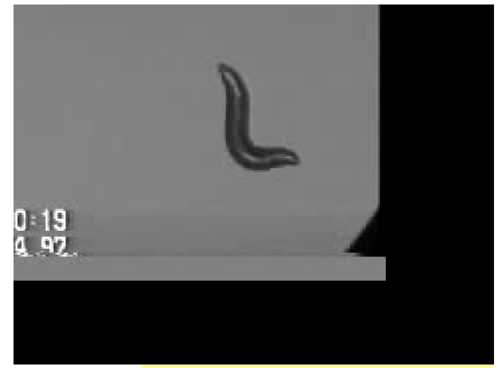
Functional circuits of C Elegans

- **Touch sensitivity**
- **Egg laying**
- **Thermotaxis**
- **Chemosensory**
- **Defecation**
- **Locomotion when**
  - **Satiated: Feeding**
  - **Hungry: Exploration**
  - **Escape behavior: Tap withdrawal**

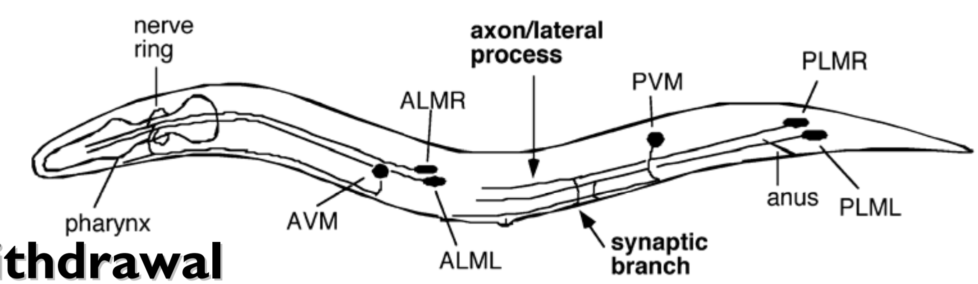
Tap Withdrawal Circuit



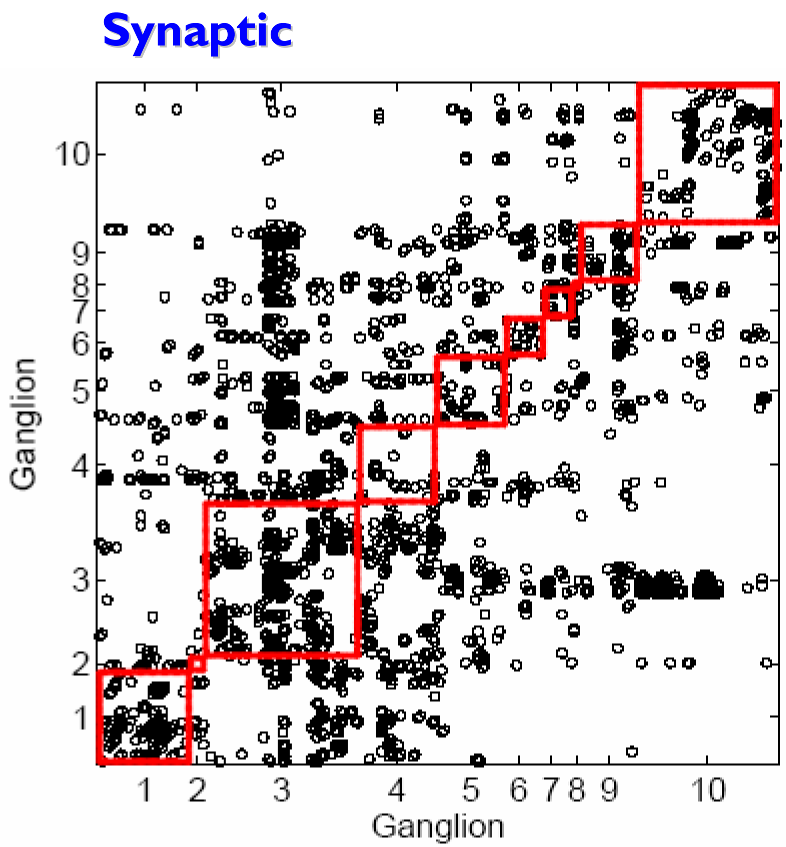


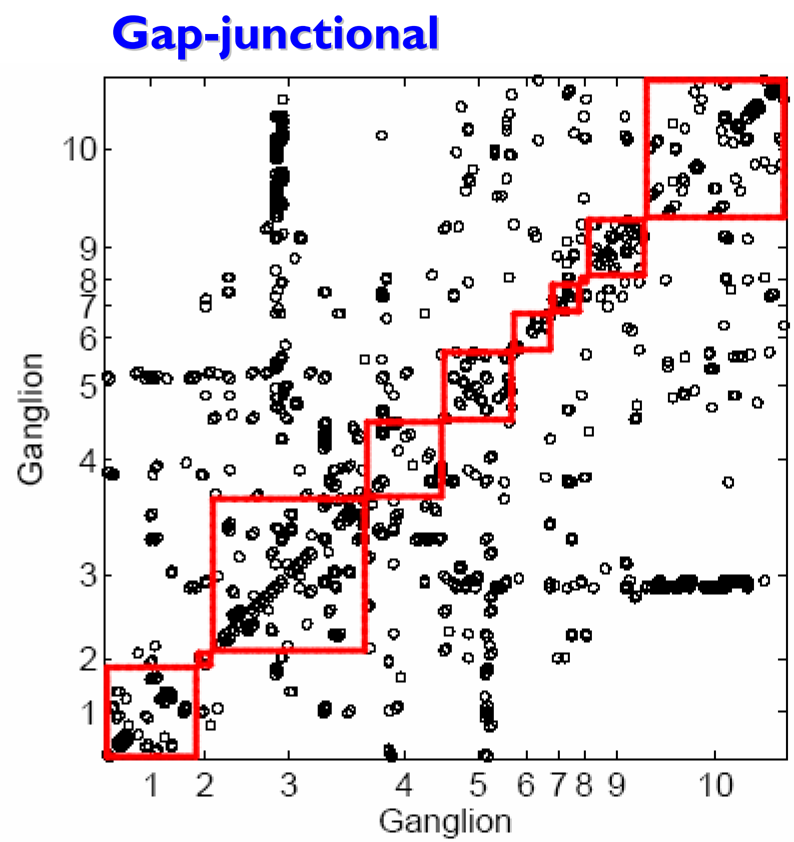


Movie,
Lockery Lab



Connectivity of the somatic nervous system





Question:

Is the network modular ?

How do you determine the modules if the connections are not localized within corresponding ganglia ?

Measuring modularity

How to quantify the degree of modularity ?

One suggested measure:

$$Q \equiv \frac{1}{2L}\sum_{i,j}\left[A_{ij} - \frac{k_i k_j}{2L}\right]\delta_{c_i c_j}$$ (Newman, EPJB, 2004)

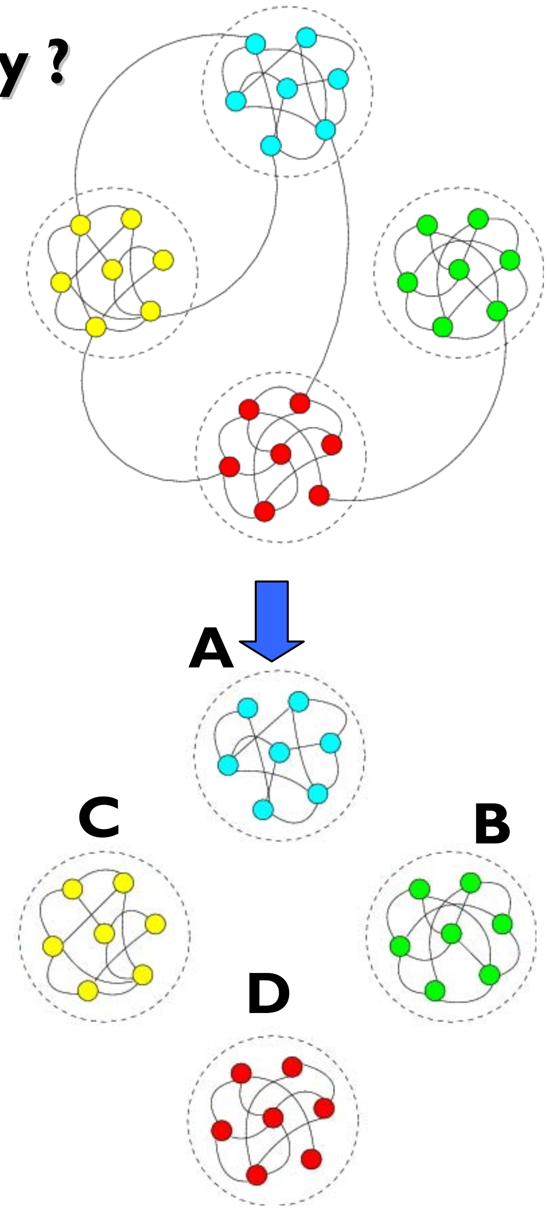
A: Adjacency matrix
L : Total number of links
k_i : degree of *i*-th node
c_i : label of module to which *i*-th node belongs

For directed & weighted networks:

$$Q^W \equiv \frac{1}{L^W}\sum_{i,j}\left[W_{ij} - \frac{s_i^{\text{in}} s_j^{\text{out}}}{L^W}\right]\delta_{c_i c_j} \qquad (L^W = \textstyle\sum_{i,j} W_{ij})$$

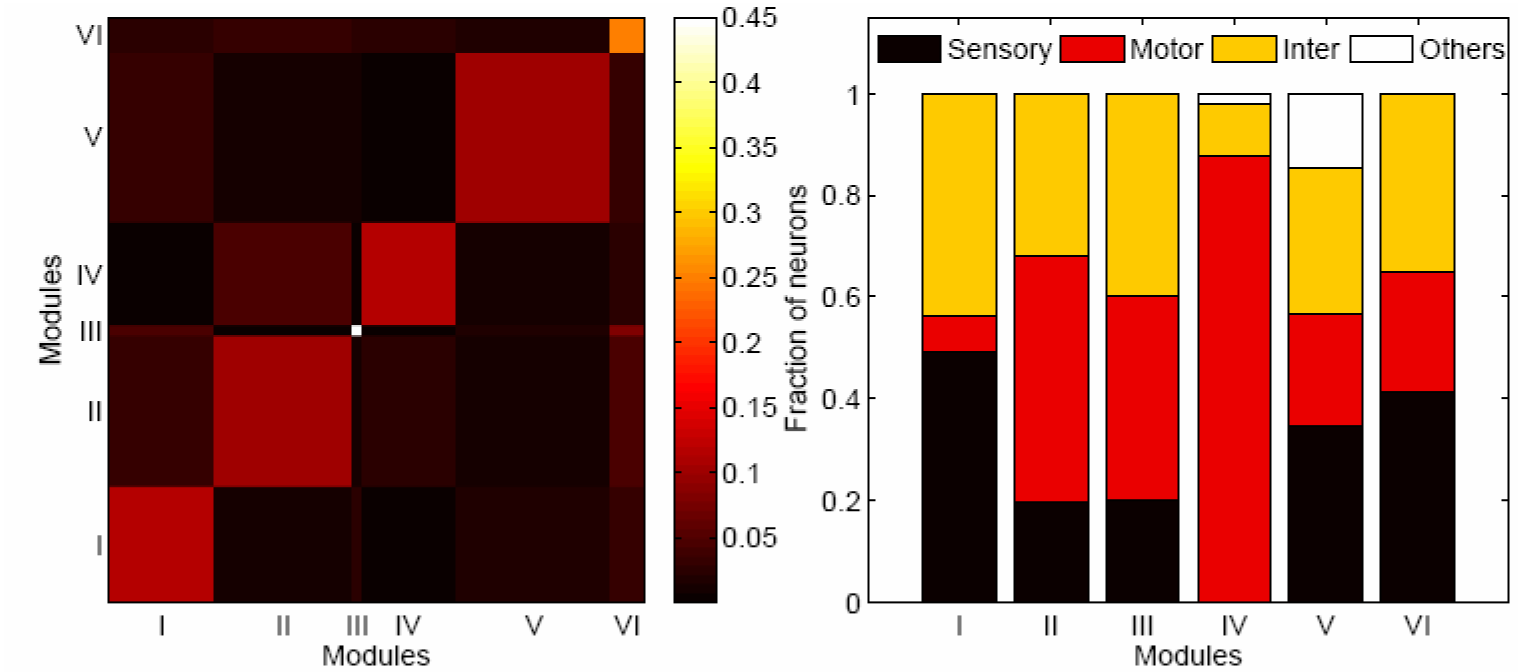
W: Weight matrix
s_i : strength of *i*-th node

Modules determined through a generalization of the spectral method (Leicht & Newman, 2008)



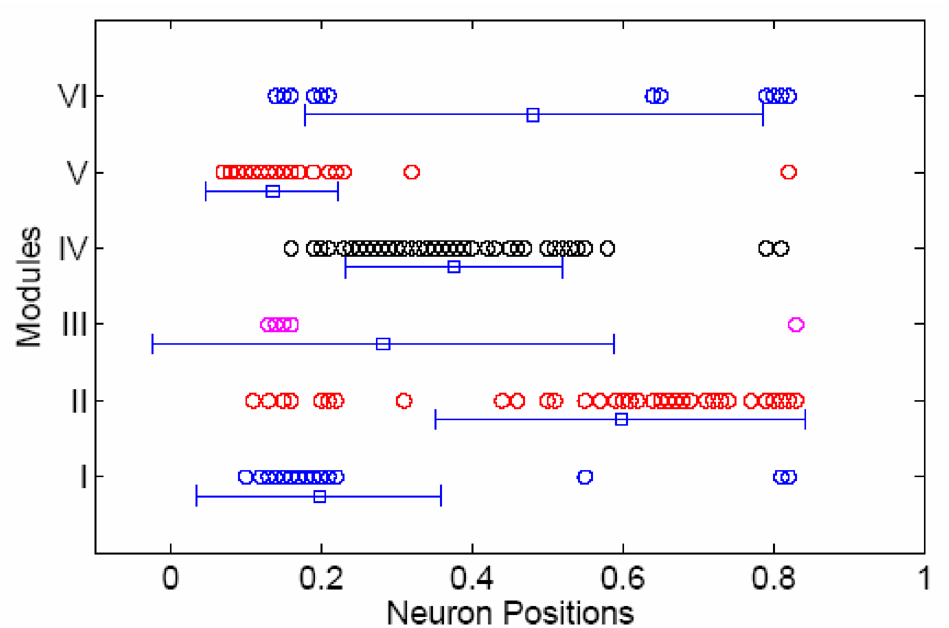
The Modular Structure of the Network

Optimal decomposition of the somatic nervous system into 6 modules



- Dense interconnectivity within neurons in a module, relative to connections between neurons in different modules
- The modules are not simply composed of one type of neurons (e.g., a purely sensory neuron or motor neuron or interneuron module does not exist)

Modules and Spatial Localization



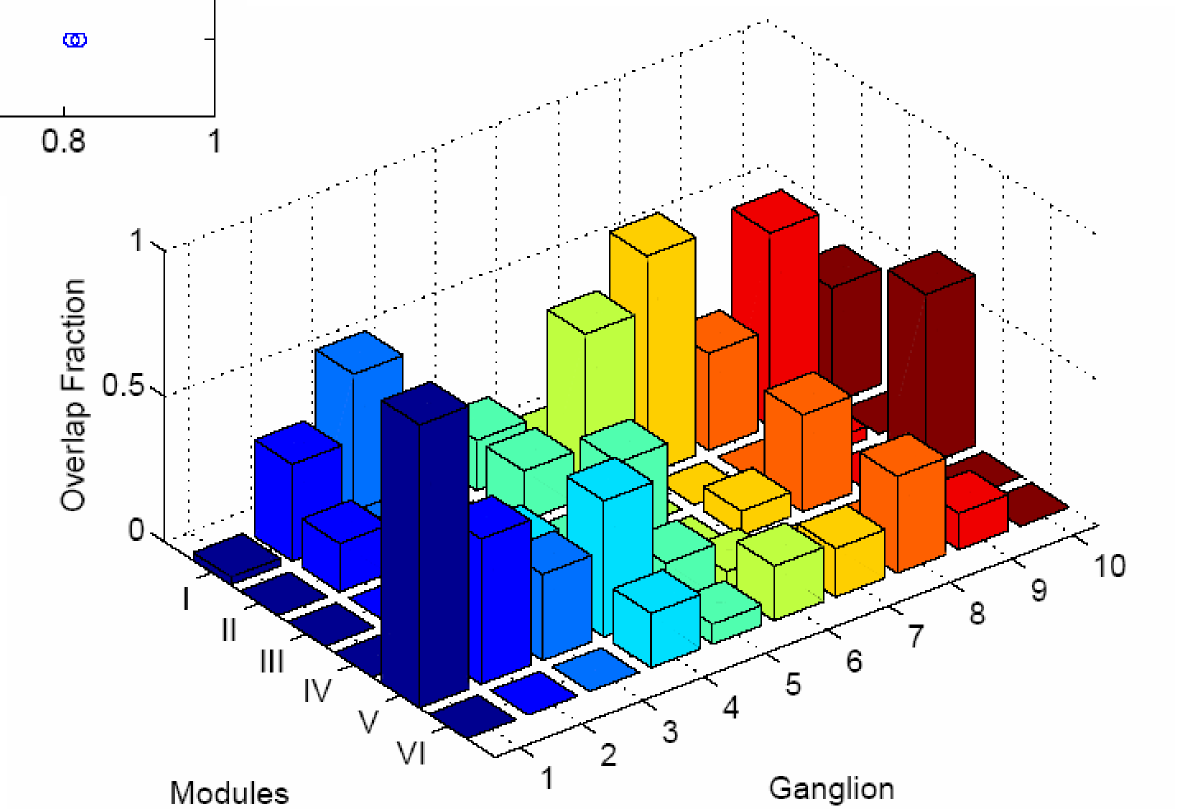
Q. Do constraints related to physical adjacency of neurons (e.g., minimization of wiring length) completely explain the modular organization ?

Ans. NO

Q. Does the existence of ganglia explain the modules ?

Ans. NO

Most ganglia are composed of neurons belonging to many different modules

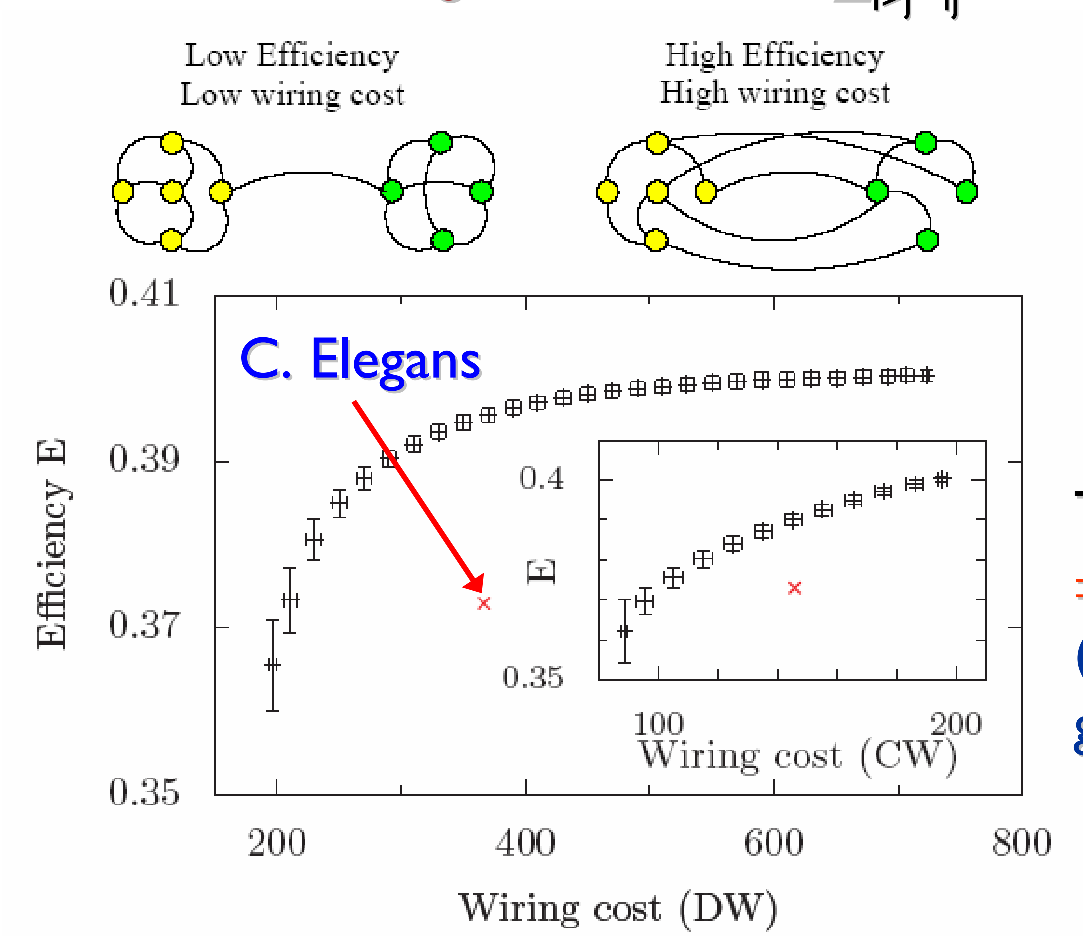


Optimizing for wiring cost and communication efficiency

Communication efficiency $E = 1 / \text{avg path length}, \ \ell = 2/N(N-1) \sum_{i>j} d_{ij}$

Wiring cost $DW = \sum_{i>j} d_{ij}$ for all connected neurons

("dedicated wire" model)



Trade-off between increasing communication efficiency and decreasing wiring cost

The network is **sub-optimal !**

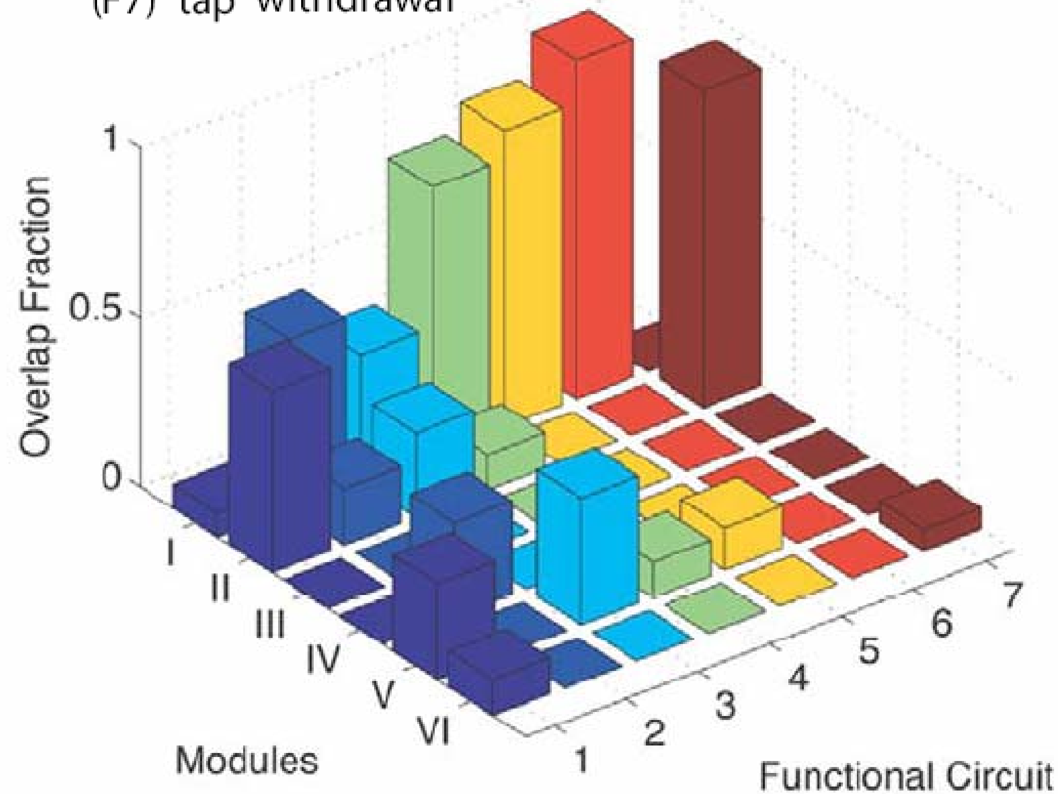
⇒ presence of other constraints (possibly related to function) governing network organization

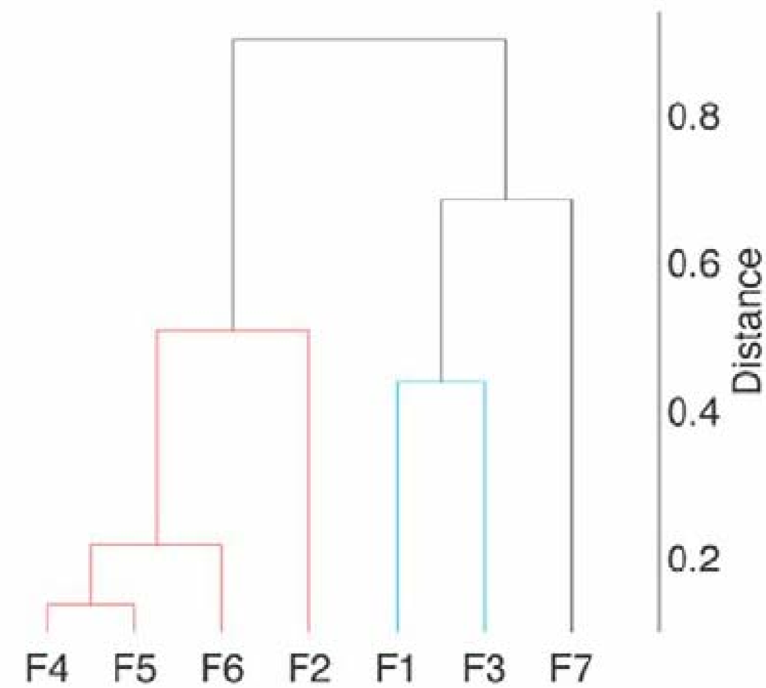
Modules and Functional Circuits

(F1) mechanosensation
(F2) egg laying
(F3) thermotaxis
(F4) chemosensation
(F5) feeding
(F6) exploration
(F7) tap withdrawal

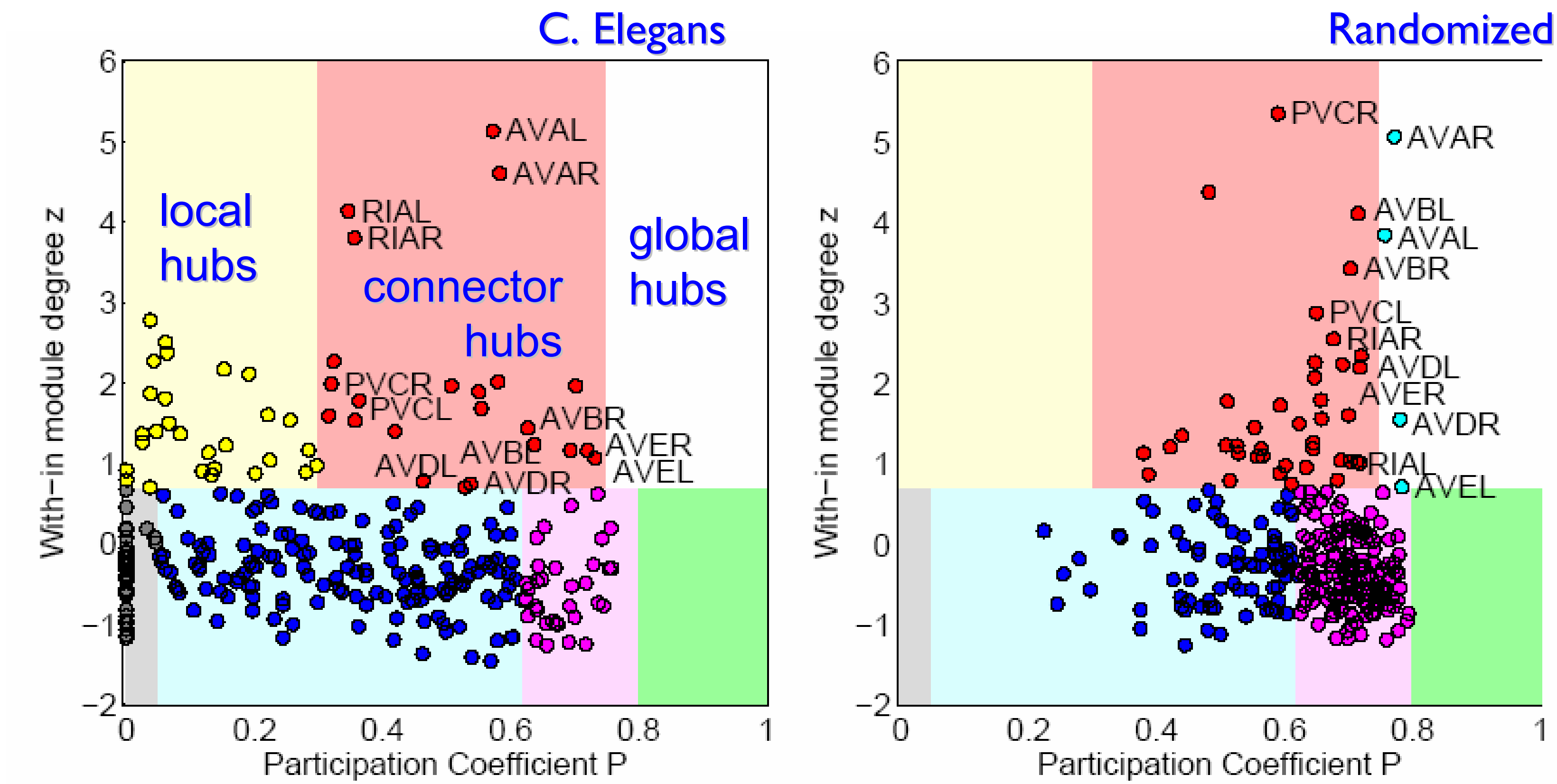
Overlap between module & functional circuit measured by fraction of neurons common

Closeness among functional ckts in 6-D “modular” space ⇒F2 close to (F4,F5,F6) *Supported by exptl observation*: presence of food detected through chemosensory neurons modulates the egg-laying rate in C. elegans





Mesoscopic network structure can alert us to critical functional role of certain neurons



Importance of connector hubs: possibly integrating local activity for coherent response, 21 out of 23 already implicated in critical functions

***Prediction*: AVKL and SMBVL are likely important for some as yet undetermined function**

Q. What mesoscopic structure ?
Ans. Modular

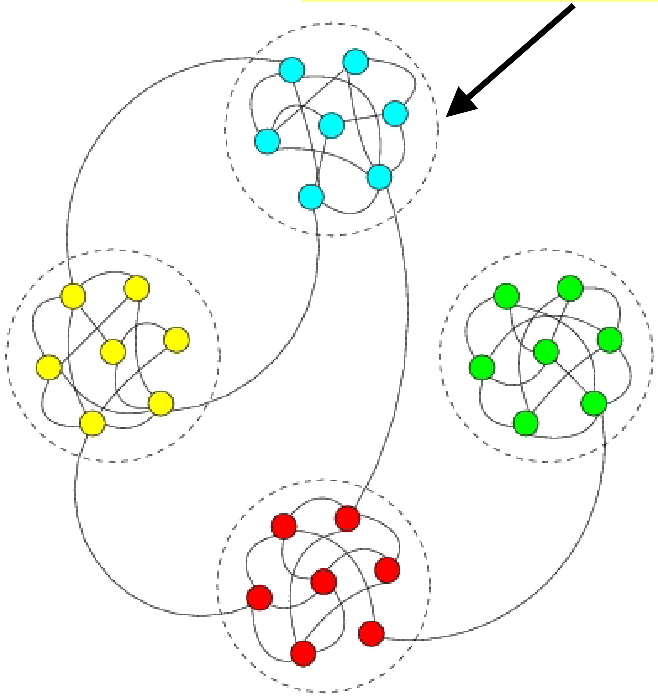
Q. How do such structures affect dynamics ?

Over networks, such dynamics can be of

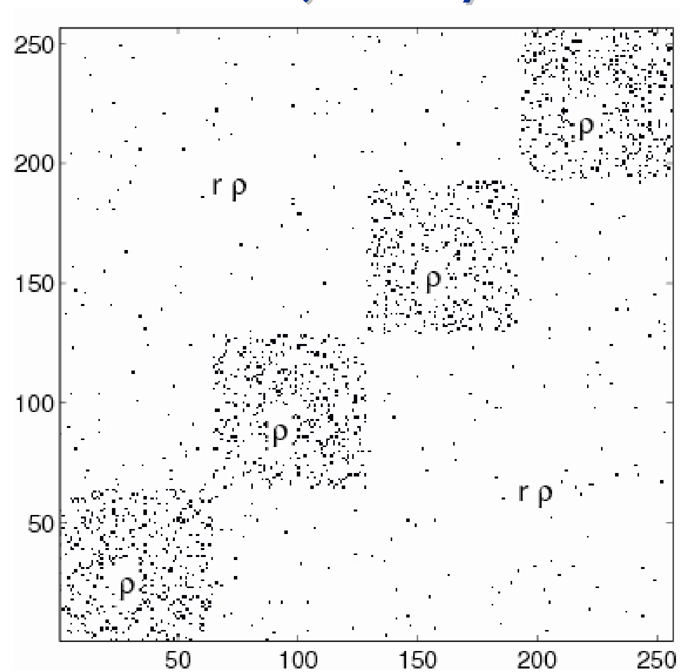
- synchronization
- consensus or opinion formation
- information or epidemic spreading
- adoption of innovations

A simple model of modular networks

Module ≡ random network



Adjacency matrix



Model parameter *r* : Ratio of inter- to intra-modular connectivity

The modularity of the network is changed keeping avg degree constant

Modular networks ≡ Small-World Networks

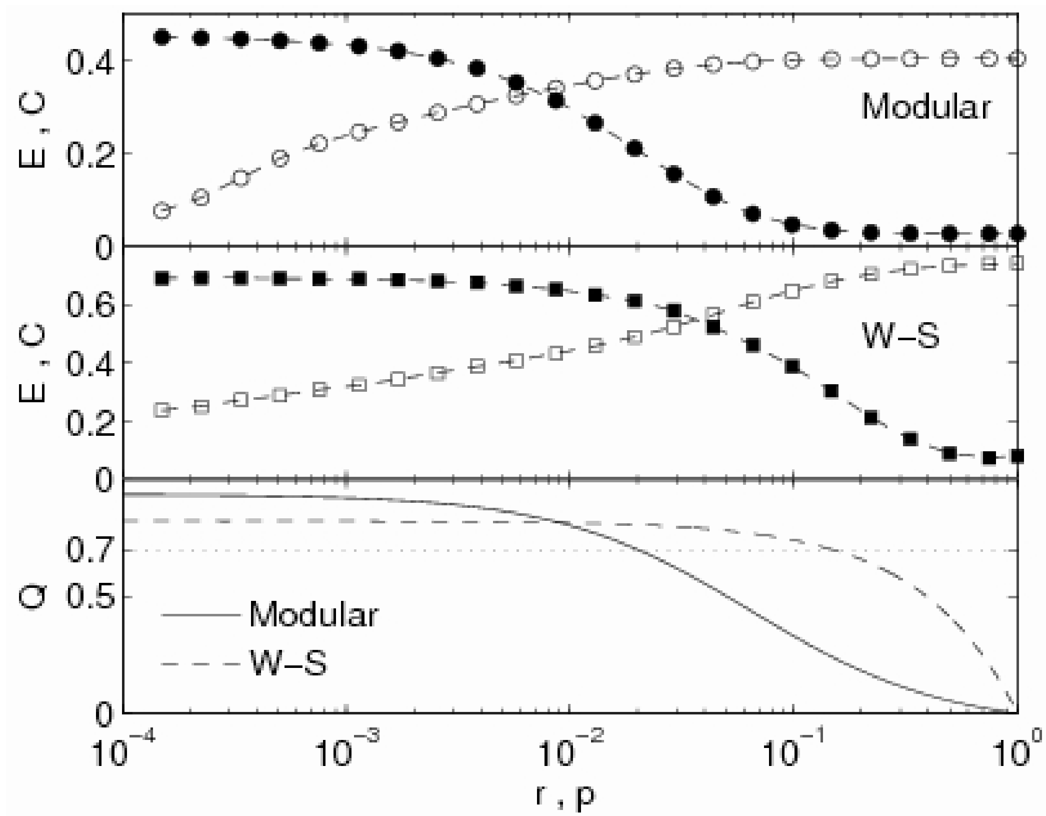
Structural measures for characterizing SW networks:

Communication efficiency **E = 1 /avg path length, $\ell = 2/N(N-1) \sum_{i>j} d_{ij}$**

Clustering coefficient **C = fraction of observed to potential triads**
$= (1/N) \sum_i 2n_i / k_i (k_i - 1)$

Watts-Strogatz and Modular networks behave similarly as function of *p* or *r*

(Also between-ness centrality, edge clustering, etc)



Then how can you tell them apart ?

Dynamics on Watts-Strogatz network different from that on Modular networks

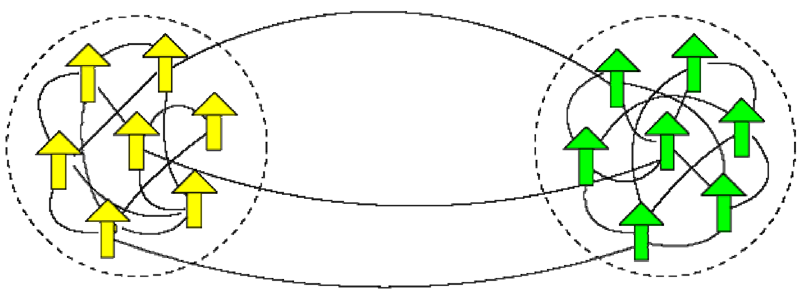
Network topology

Consider *ordering* or alignment of orientation on such networks

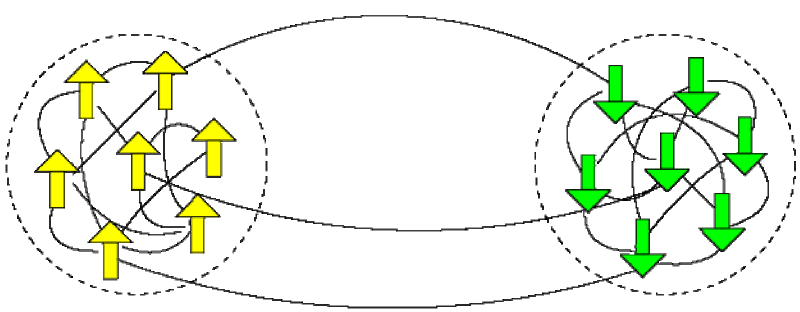
e.g., Ising spin model: dynamics minimizes $H = - \sum J_{ij} S_i(t) S_j(t)$

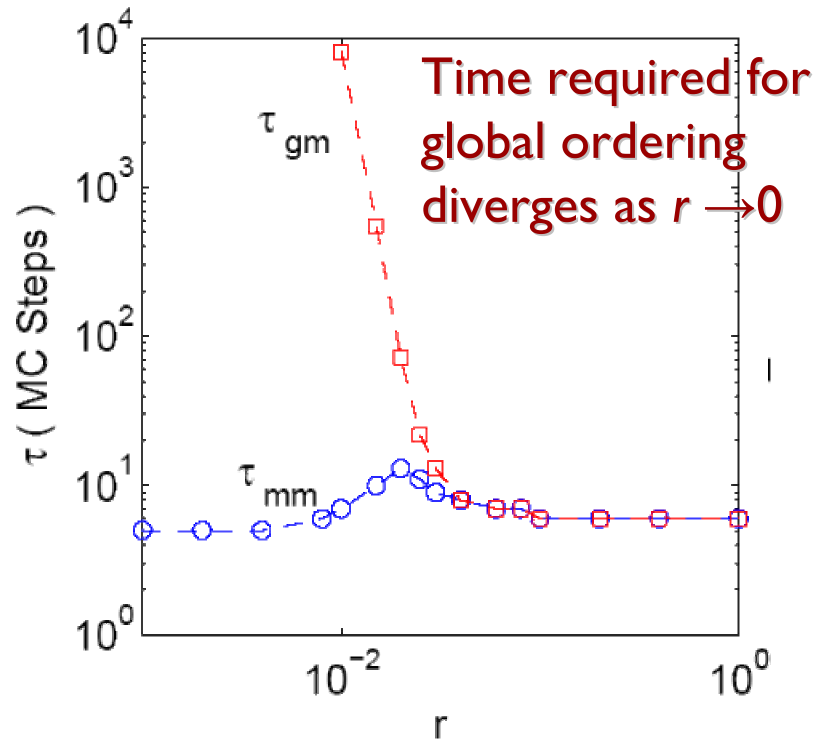
2 distinct time scales in Modular networks: $t_{modular}$ & t_{global}

Global order



Modular order





Universality

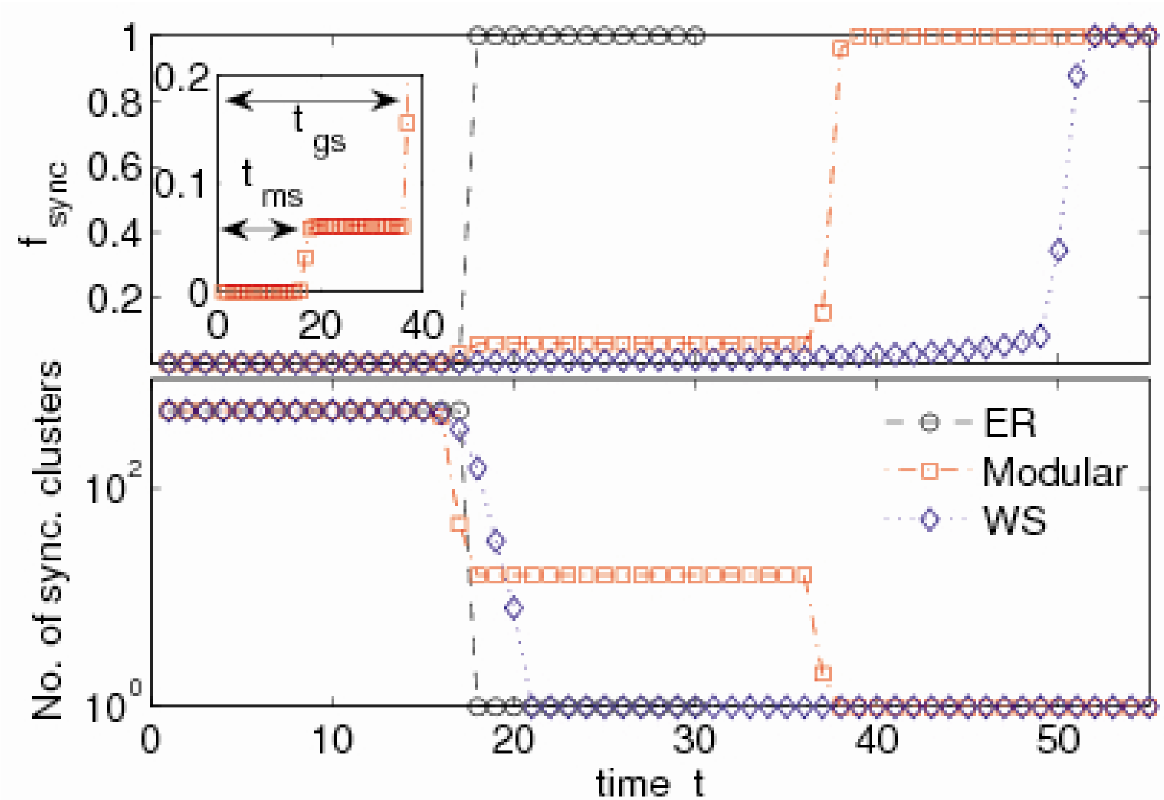
Almost identical multiple time scale behavior is seen for nonlinear oscillator synchronization

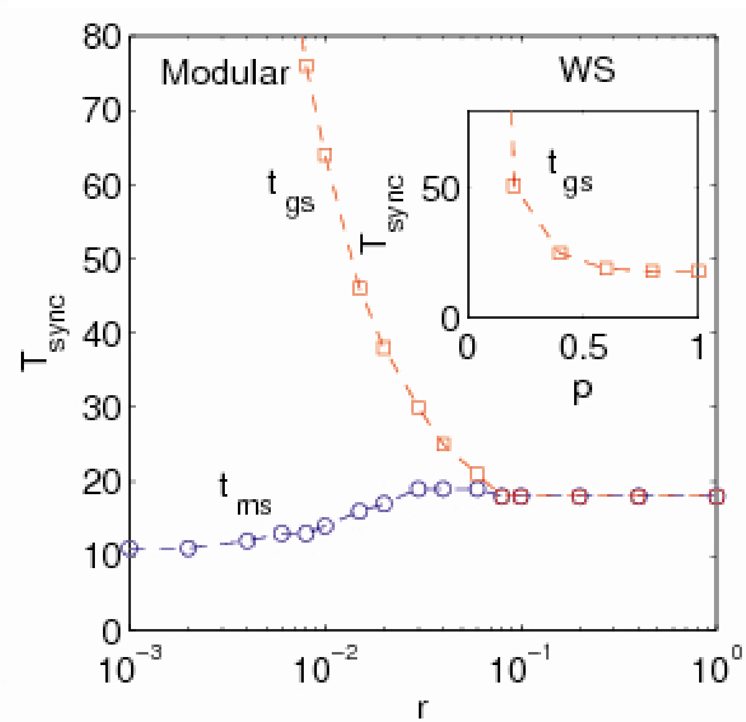
Network topology

Consider synchronization on modular networks

e.g., Kuramoto oscillators: $d\theta_i/dt = w + (1/k_i)\sum K_{ij} \sin(\theta_j - \theta_i)$

2 distinct time scales in Modular networks: $t_{modular}$ & t_{global}





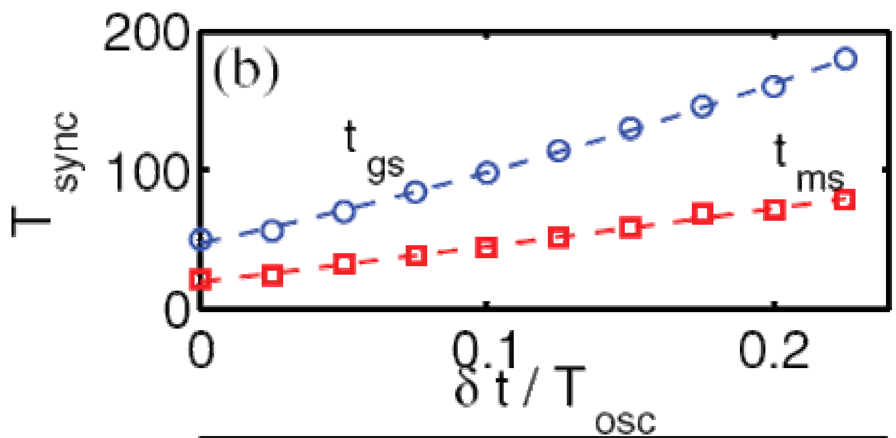
Universality: Presence of delay

Delays in coupling also show the multiple time-scales in synchronization

coupling term changes to

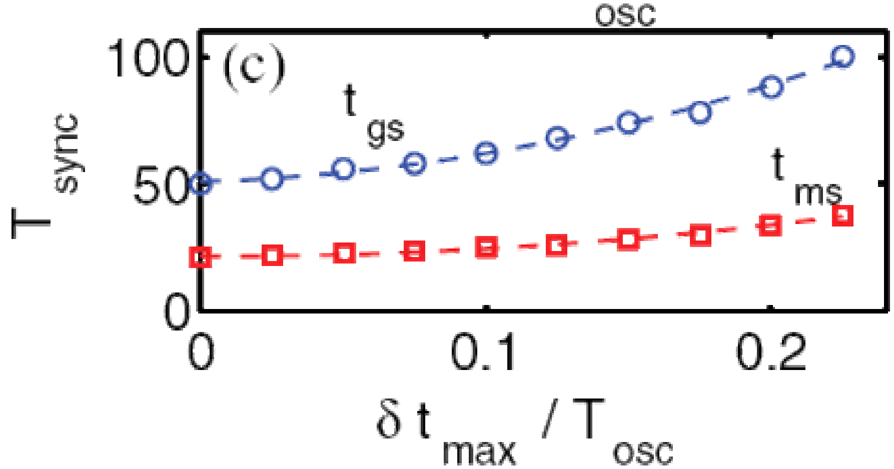
$$\sum_{j=1}^{N} \frac{K_{ij}}{k_i}[x_j(t-\delta t) - x_i(t)]$$

N=512, m=16, <k> = 14, r = 0.02



Constant delay

(all inter- & intra-modular links)



Random inter-modular delay

Laplacian Analysis

Time-evolution of a network of *n* identical oscillators

$$\dot{x}_i = F(x_i) + \underbrace{\epsilon}_{\text{Coupling strength}} \sum_{j=1}^{n} \underbrace{L_{ij}}_{\text{Laplacian}} H(x_j)$$

$$\begin{aligned} L_{ii} &= k_i, \text{ the degree of node } i, \\ L_{ij} &= -1 \text{ if nodes } i \text{ and } j \text{ are connected} \\ &= 0, \text{ otherwise.} \end{aligned}$$

Laplacian Eigenvalues: $0 = \lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n$

Pecora & Carroll, 1998: A synchronized state is linearly stable iff the eigenratio $\lambda_N/\lambda_2 < \alpha_B/\alpha_A$, ratio of bounds of effective couplings

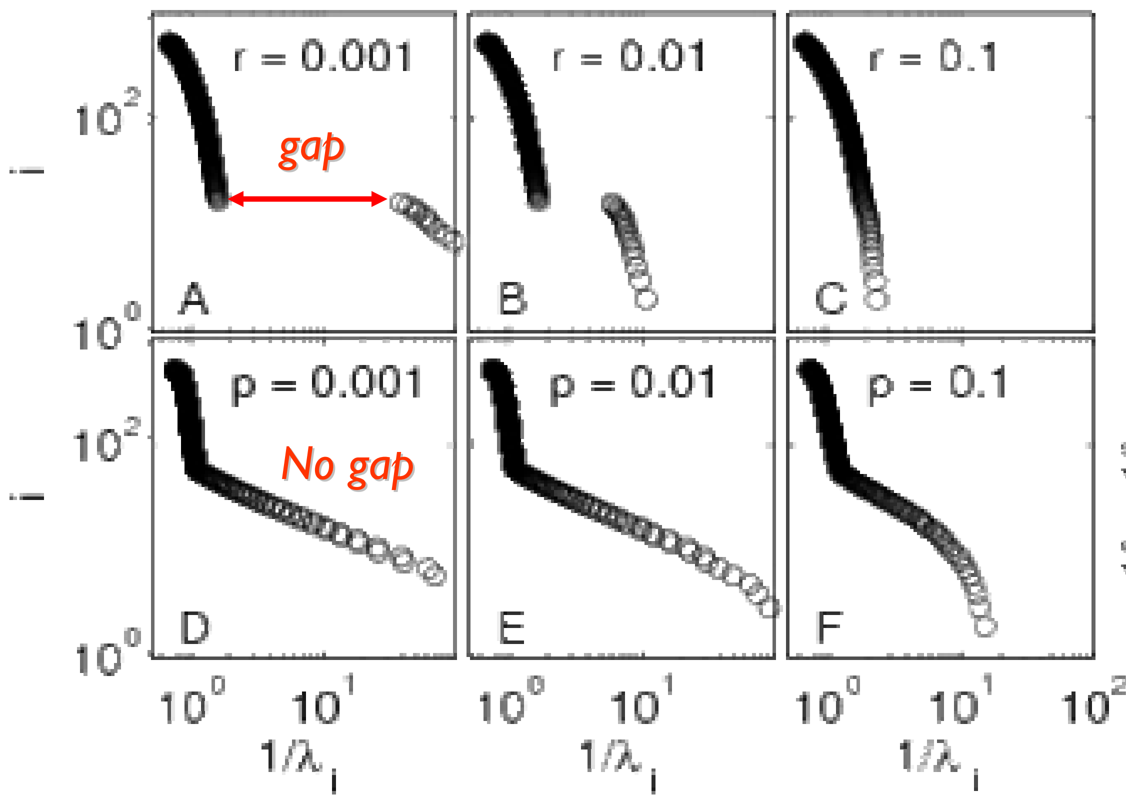
$\Rightarrow$ Network with smaller λ_N/λ_2 more likely to show stable synchronization

Dynamics of normal modes around synch $\varphi_i(t) = \sum_j B_{ij}\theta_j = \varphi_i(0)\exp^{-\lambda_i t}, i = 1, \ldots, N$

Eigenvalue spectra of the Laplacian

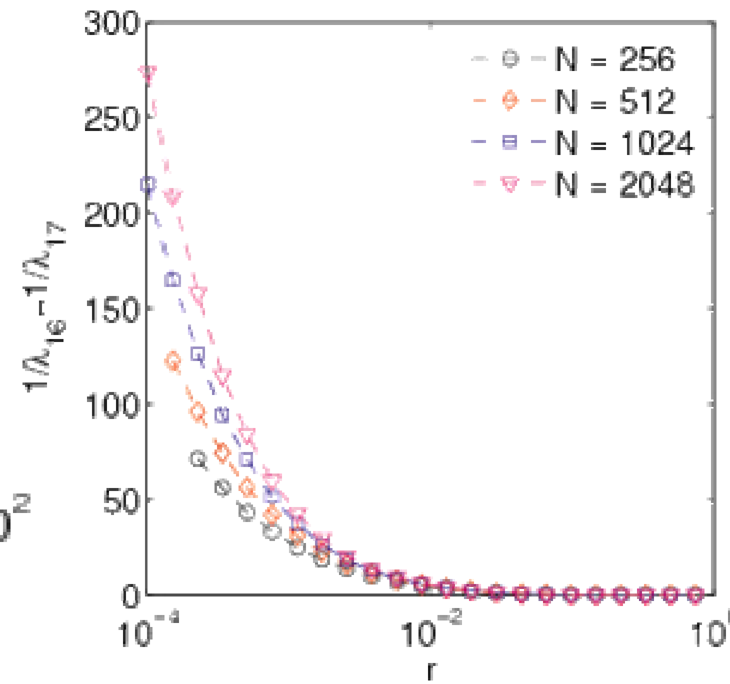
Shows the existence of spectral gap ⇒ distinct time scales

Modular network Laplacian spectra



Watts-Strogatz network Laplacian spectra

Spectral gap in modular networks diverges with decreasing r



Existence of distinct time-scales in Modular networks

No such distinction in Watts-Strogatz small-world networks

Diffusion process on modular networks

Random walker moving from one node to randomly chosen nghbring node

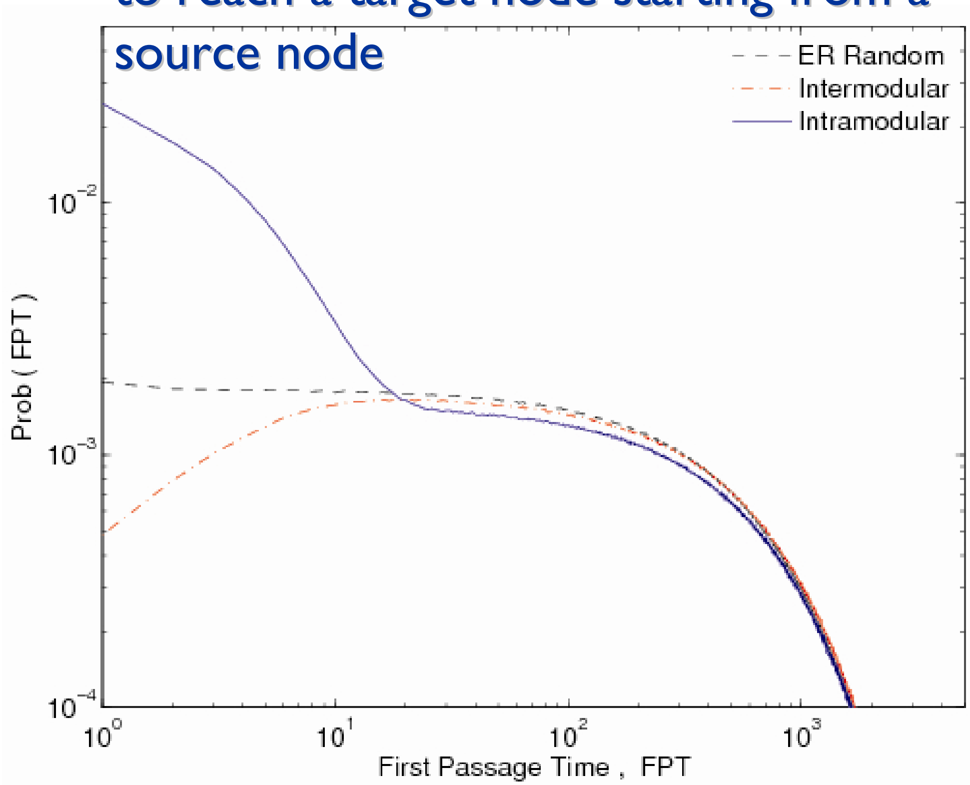
Transition probability matrix for random walk ≡ normalized Laplacian

Also shows the existence of 2 distinct time scales:

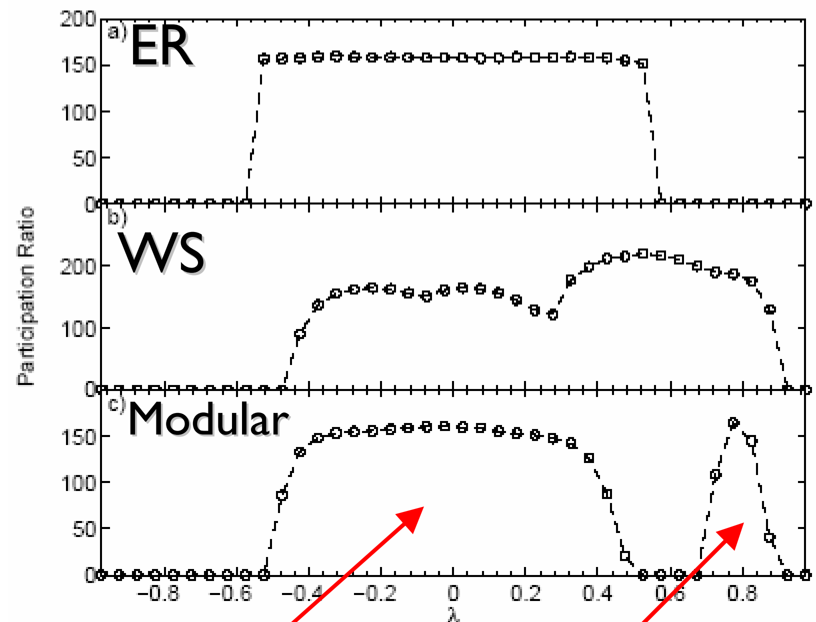
- **fast intra-modular diffusion**
- **slower inter-modular diffusion**

Relevant for diffusion of innovation or epidemics

Distrn of first passage times for rnd walks to reach a target node starting from a source node



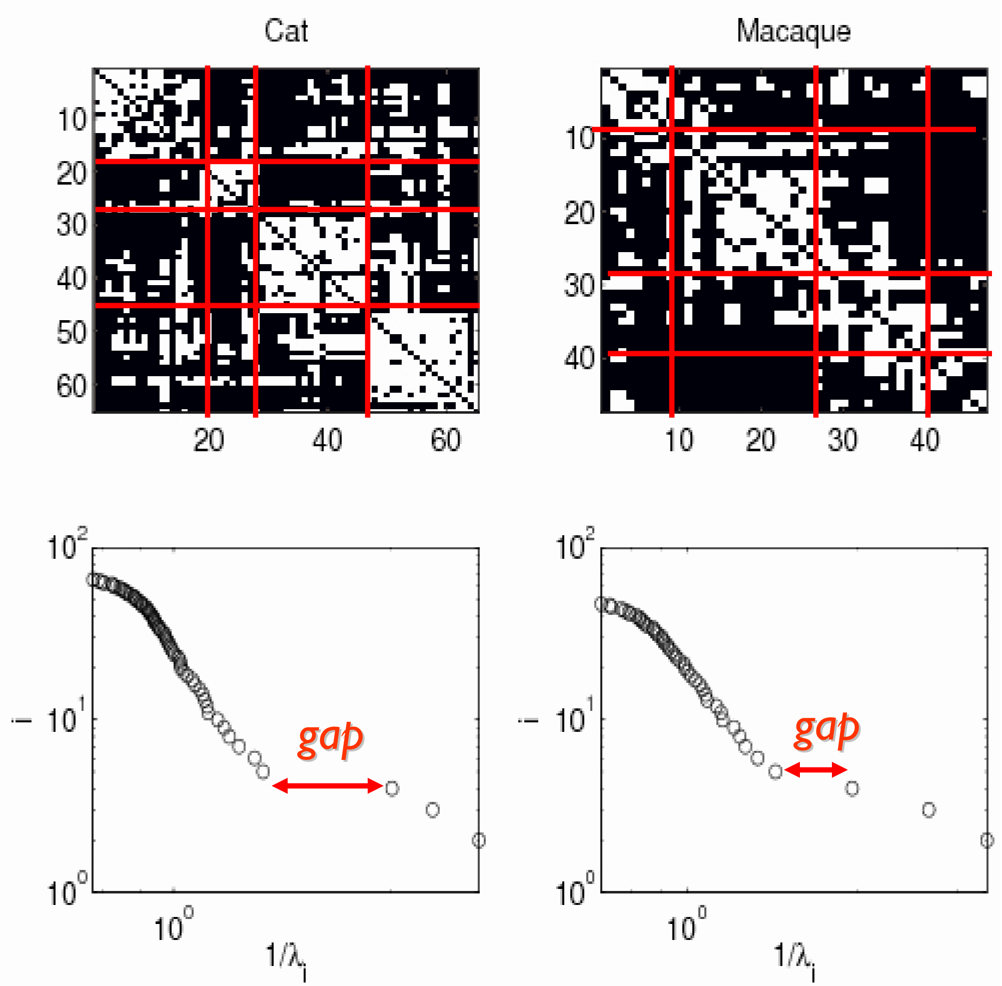
Localization of eigenmodes of transition matrix



Within modules diffusion

Between modules diffusion

How about "real" SW networks ?



The networks of cortical connections in mammalian brain have been shown to have *small-world* structural properties

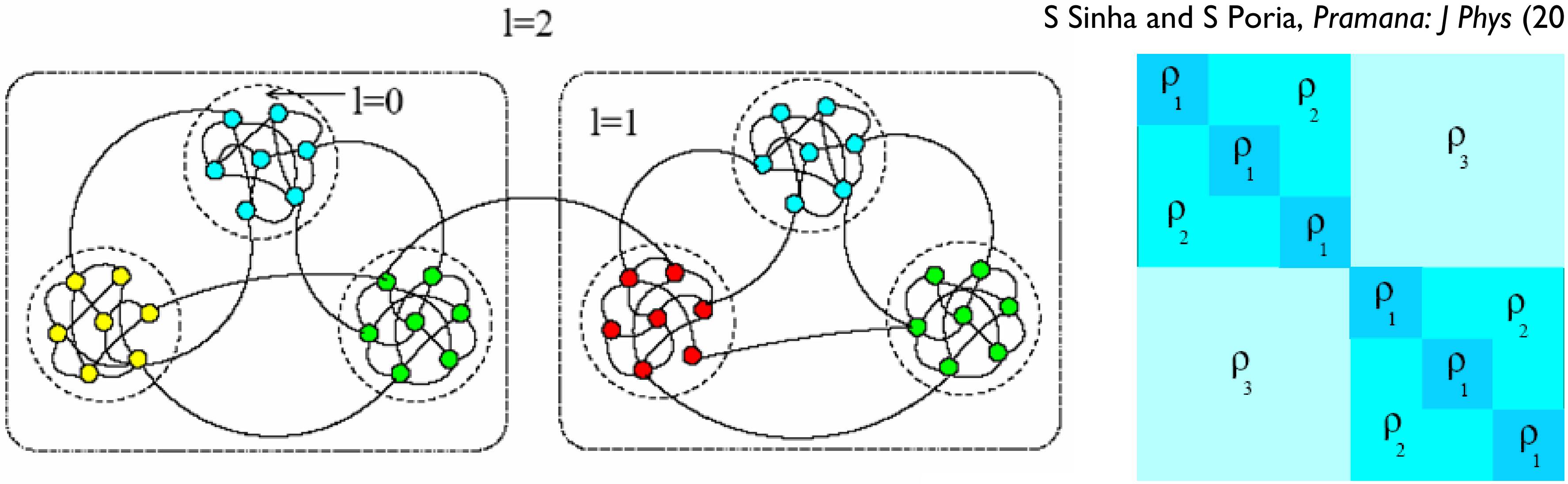
Our analysis reveals their dynamical properties to be consistent with modular "small-world" networks

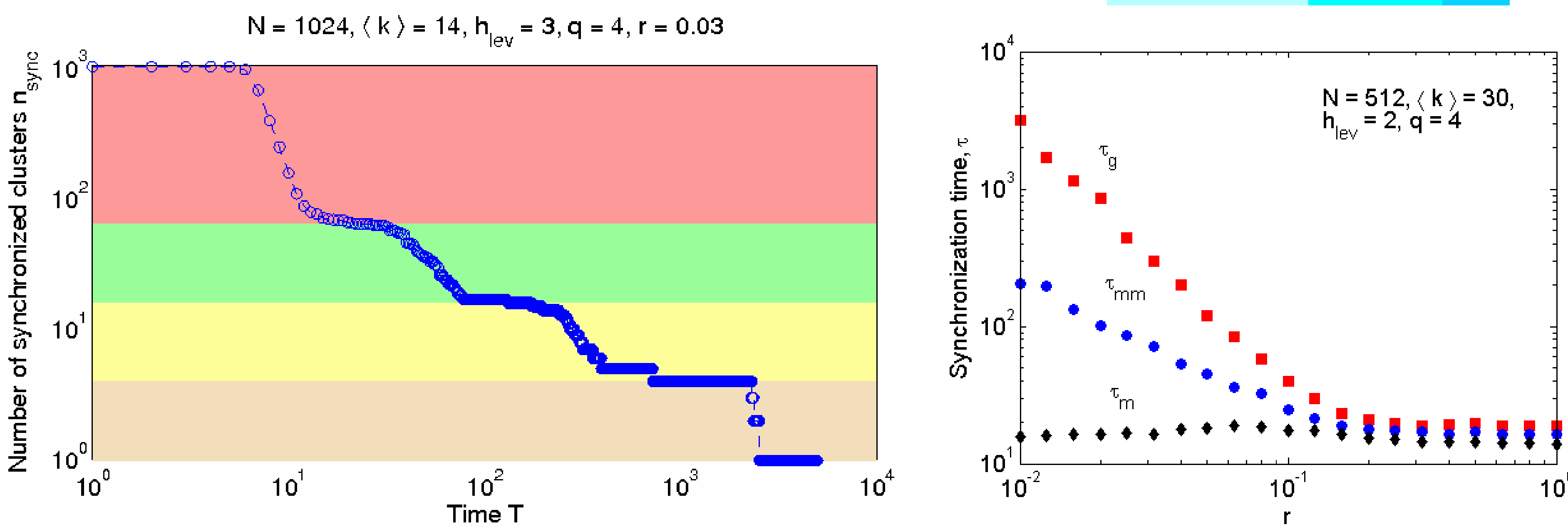
Fast synchronization of neuronal activity within a module :
The mechanism for efficient neural information processing ?

Hierarchical modular organization

introduces more dynamical time scales

S Sinha and S Poria, *Pramana: J Phys* (2011)





Consequences of meso-level structure on Dynamics

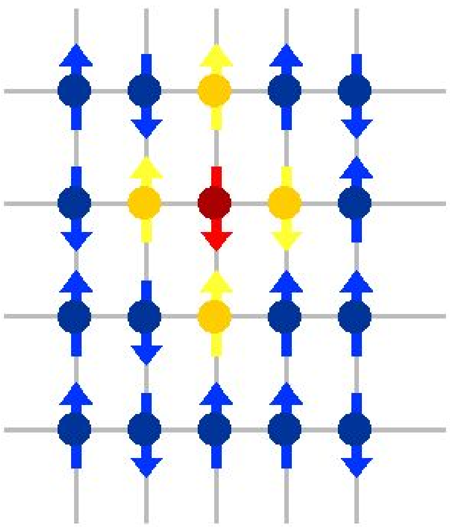
Example: consensus formation

How does individual behavior at micro-level relate to social phenomena at macro level ?

Order-disorder transitions in Social Coordination

The emergence of novel phase of collective behavior

Spin models of statistical physics: simple models of coordination or consensus formation



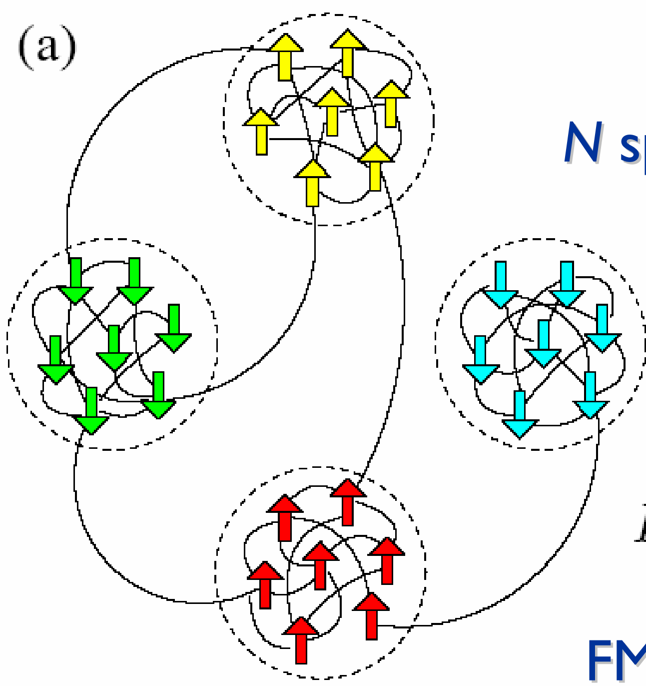
- Spin orientation: mutually exclusive choices
- Choice dynamics: decision based on information about choice of majority in local neighborhood

Simplest case: 2 possible choices

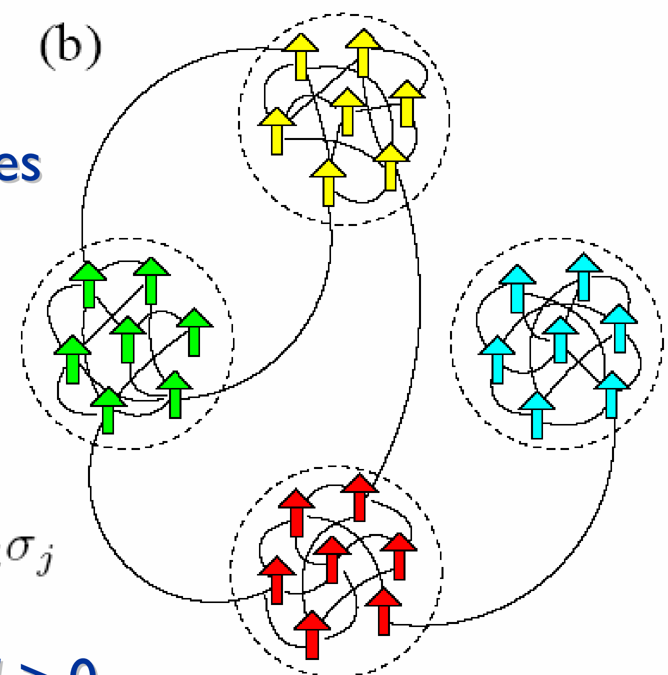
Ising model with FM interactions: each agent can only be in one of 2 states (Yes/No or +/-)

Types of possible order in modular network of Ising spins

Modular order $M_g = 0,\ \mu \neq 0$ | Global order $M_g \neq 0,\ \mu \neq 0$



N spins, n_m modules



$$H = -\sum_{i,j} J_{ij}\sigma_i\sigma_j$$

FM interactions: *J* > 0

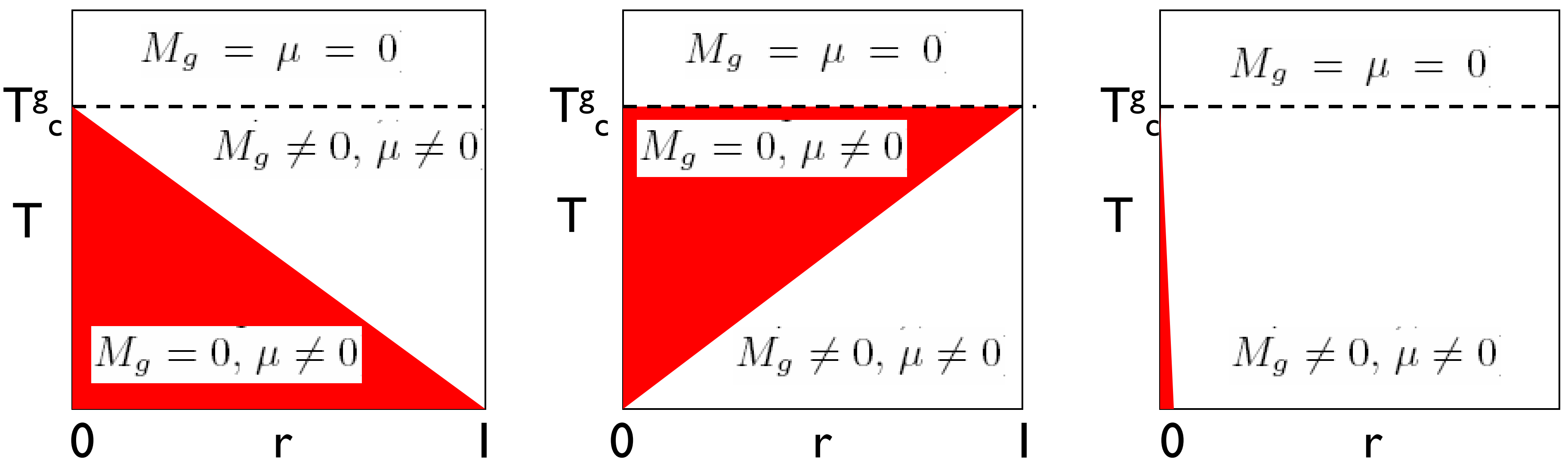
Avg magnetic moment / module $\mu = \langle | \sum_{i \in s} \sigma_i | \rangle_{s = 1, \ldots, n_m}$

Total or global magnetic moment $M_g = \sum_i \sigma_i$

Problem:

Long transient to global order can be mistaken as modular order !

Possible Phase Diagrams



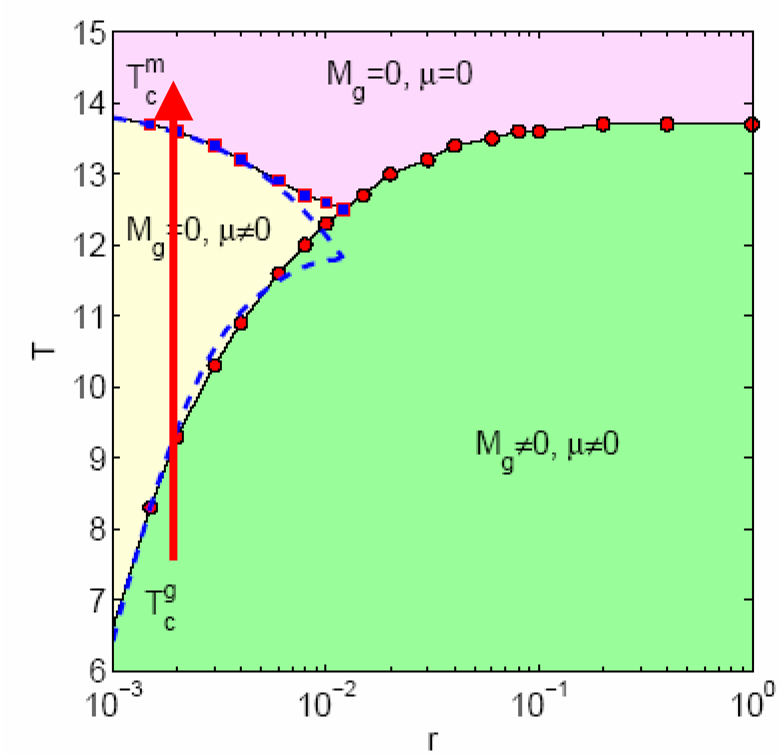
Can modular order be seen as a phase at all ?

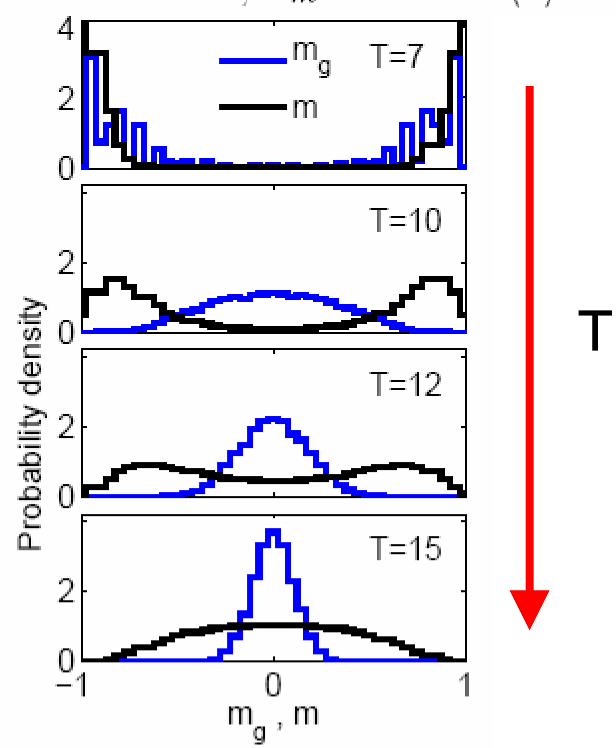
Phase diagram: two transitions

$$T_c^m = 2JL_i/(nk_B)$$

r = 0.002

$N = 512,\ n_m = 16$ and $\langle k \rangle = 14.$





$$T_c^g = \frac{J\rho_0}{k_B}(n_m - 1)n^2(2f_+ - 1)^2$$

S Dasgupta et al, PRE Rapid (2009)

There will be a phase corresponding to modular but no global order (*coexistence of contrary opinions*) even when all mutual interactions are FM (*favor consensus*) !

Even when $T < T_c^g$
strongly modular network takes very long to show global order

$\Rightarrow$Time required to achieve consensus increases rapidly for a strongly modular social organization

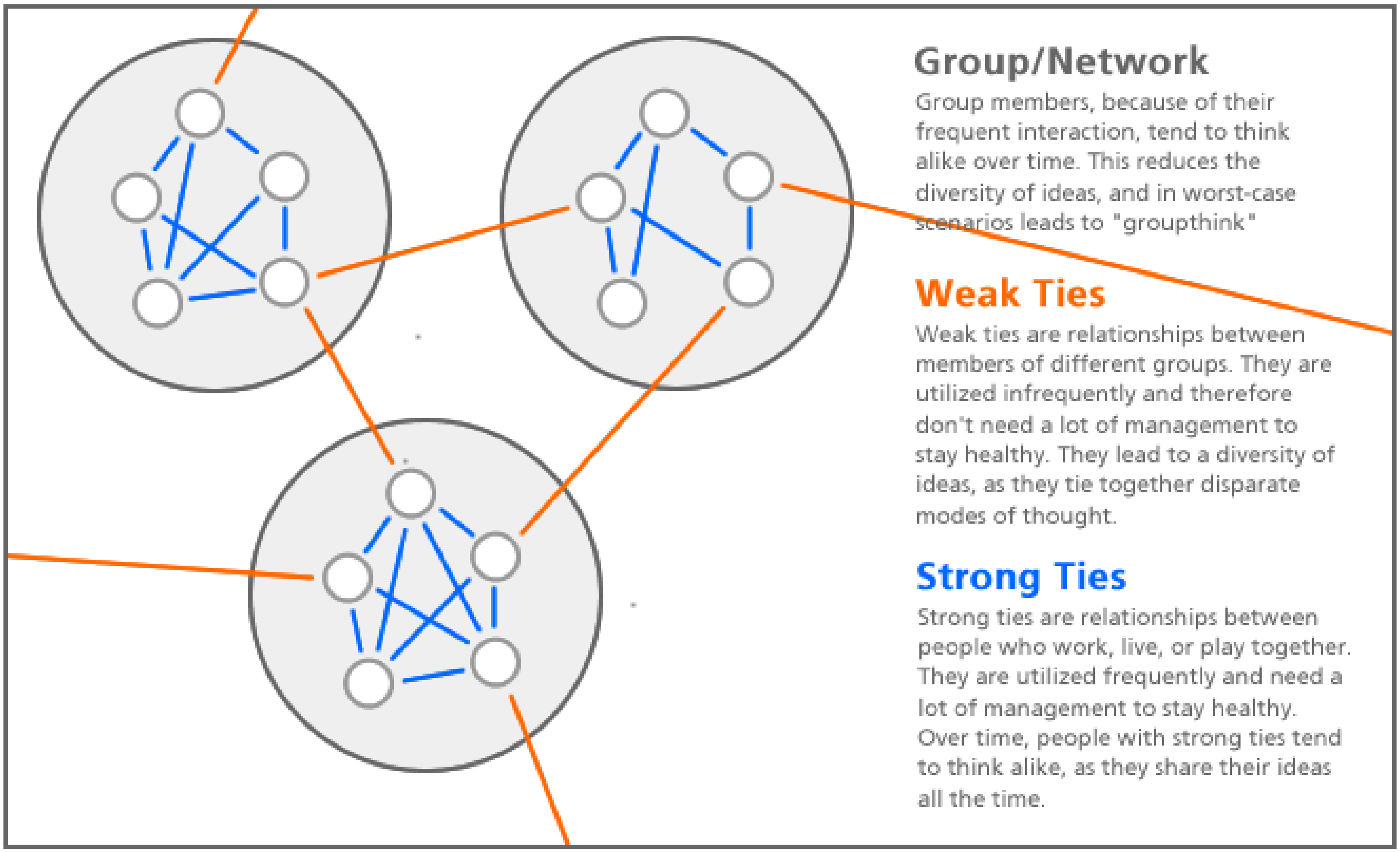
But then …
How do certain innovations get adopted rapidly ?

Possible modifications to the dynamics:

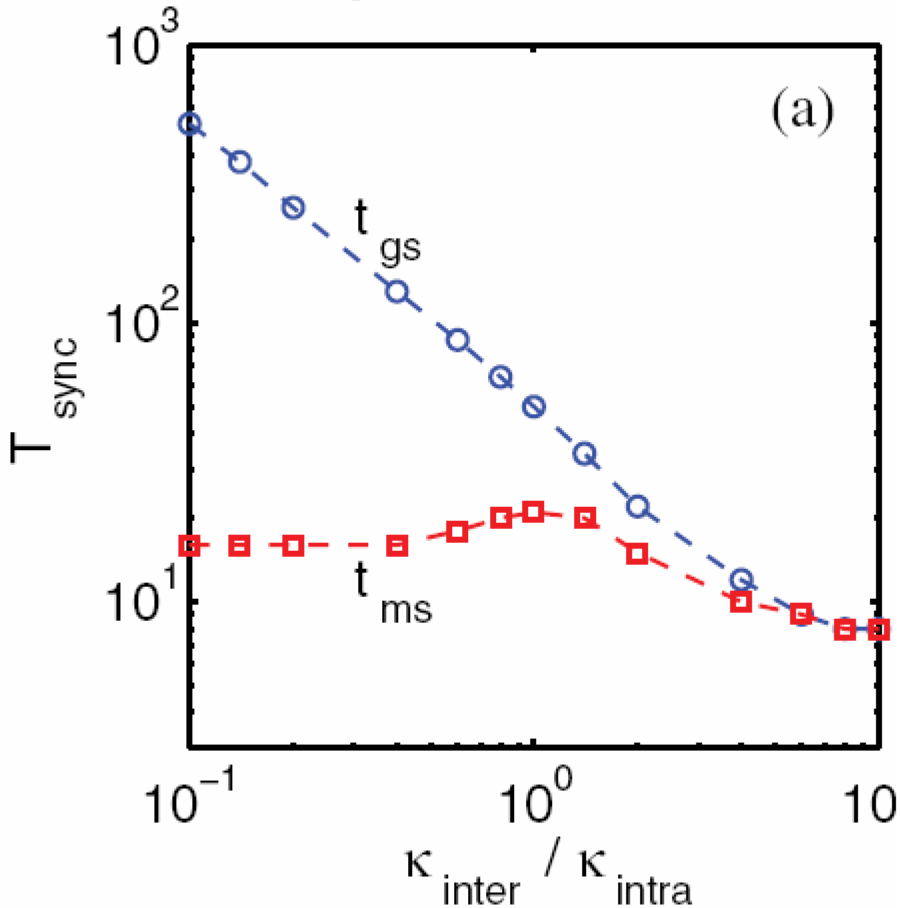
Different strengths for inter/intra couplings

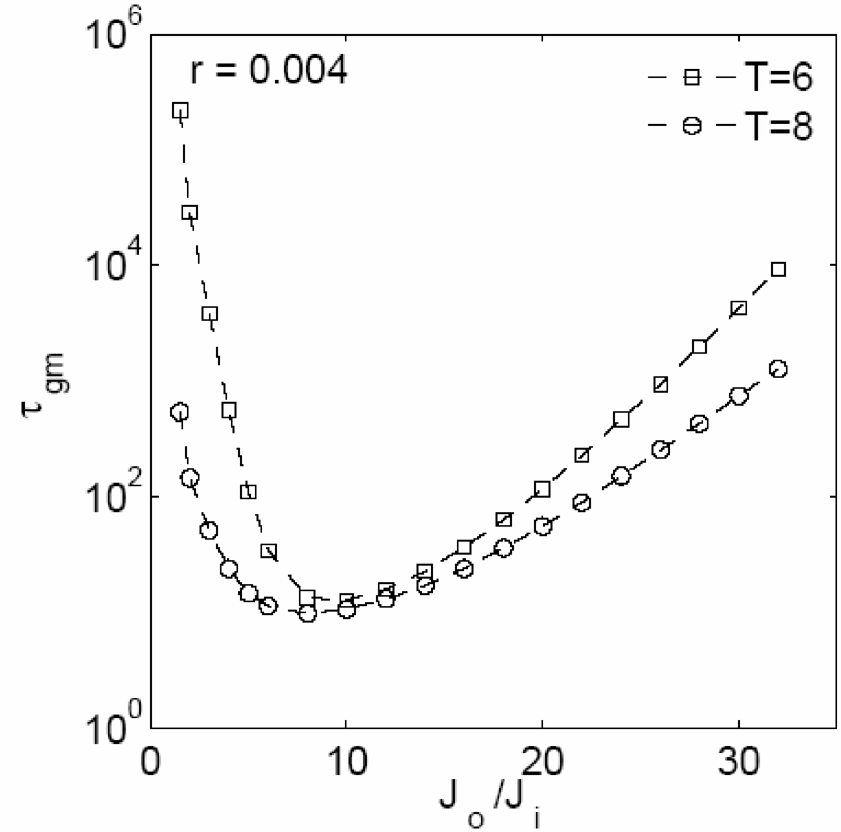
The Strength of Weak Ties: Differing Coupling Strengths Between & Within Modules

Marc Granovetter



Global Synchronization is easier with stronger inter-community links…





…But non-monotonic behavior of relaxation time with ratio of strengths of short- & long-range spin couplings

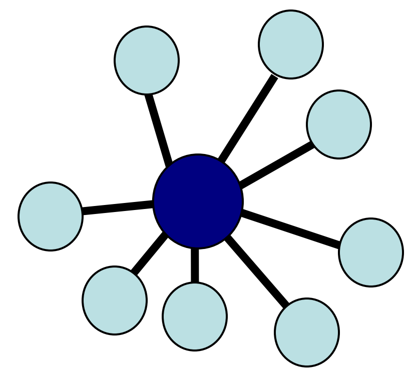
Not seen in Watts-Strogatz SW networks (Jeong et al, PRE 2005)

Why modularity ?

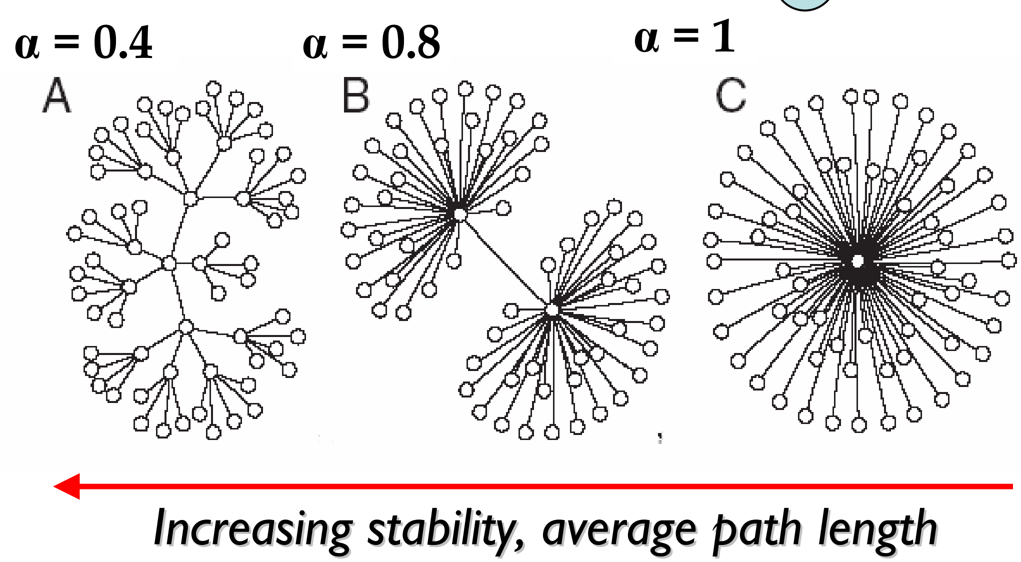
We had earlier shown that optimization under multiple (and often conflicting) network constraints can give rise to modularity

Pan and Sinha, PRE **76,** 045103(R) (2007)

- Minimizing link cost, i.e., total # links L
- Minimizing average path length ℓ
- Minimizing instability λ_{max}



Minimizing link cost and avg path length yields …
… a *star*-shaped network with single hub
But unstable !
Instability λ_{max} ~ √max degree
(i.e., degree of the hub ~ N)



***Answer:* go modular !**

…as stability increases by decreasing the degree of hub nodes λ_{max} ~ √[N/#modules]

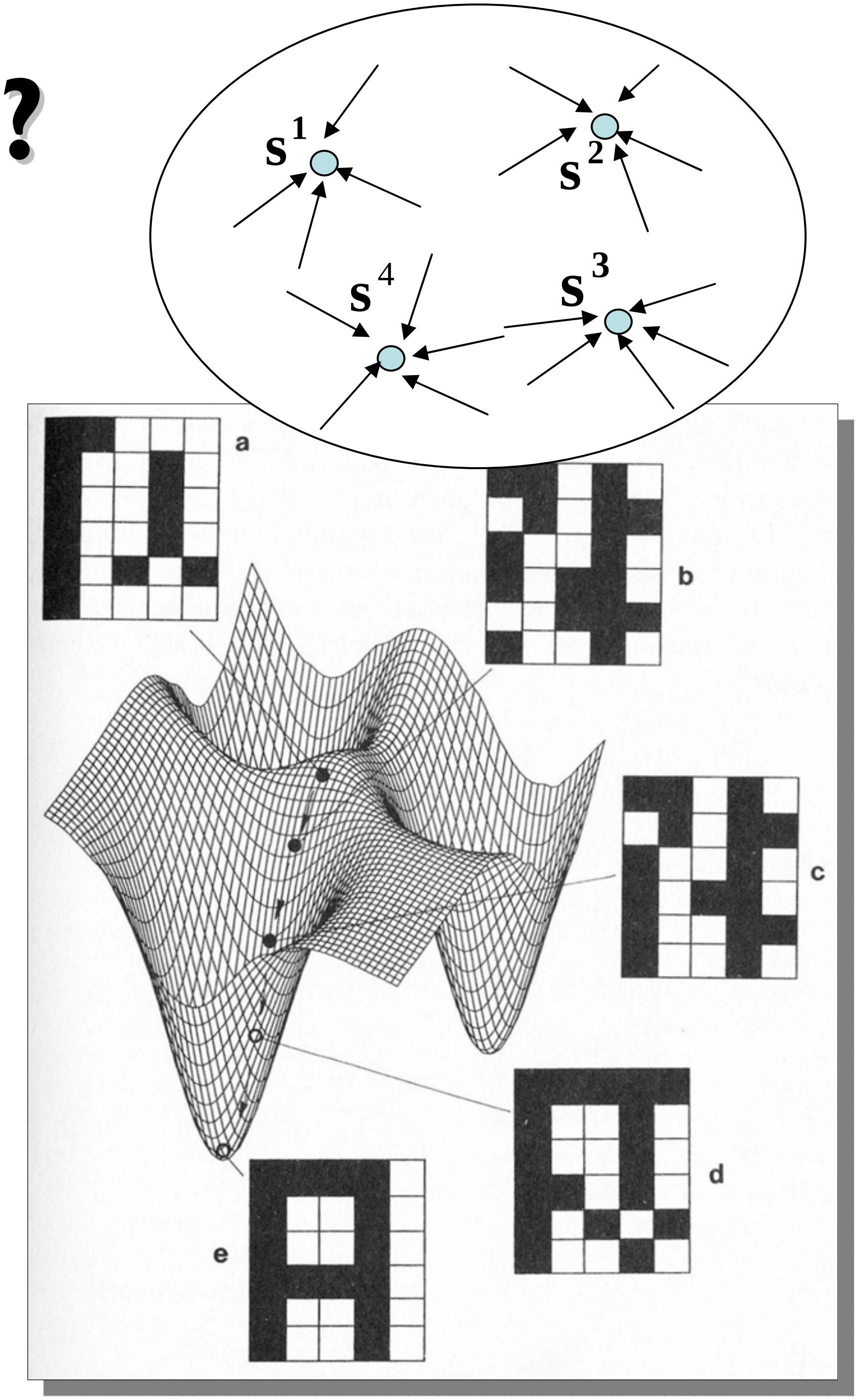
Why modularity ?

But also….

Possible utility of modularity in increasing robustness of network dynamical attractors

E.g., in the dynamics of *attractor network models* having multiple stable states ("memorized" patterns)

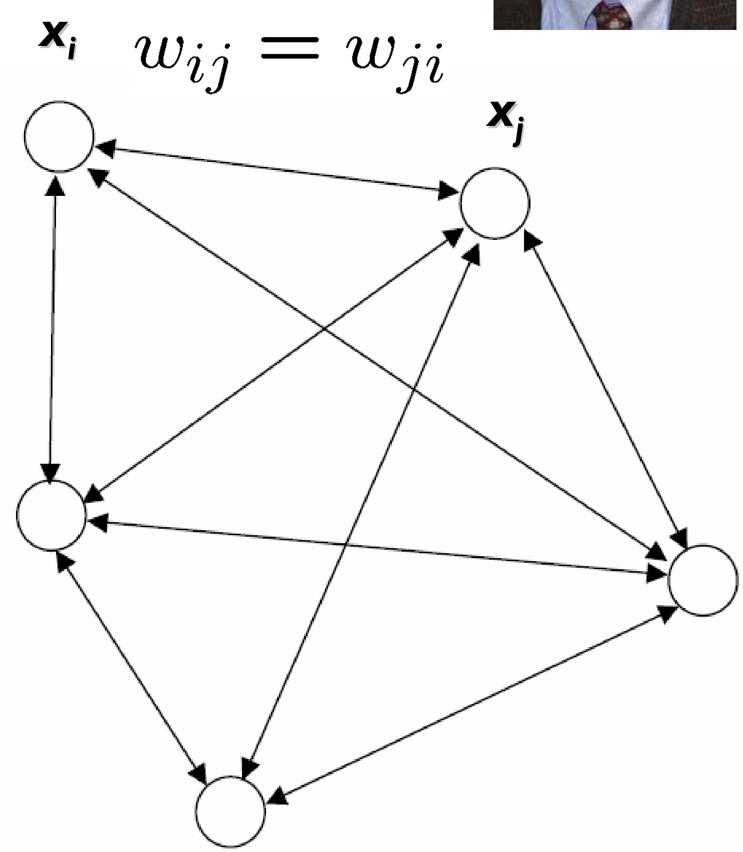
Memories ≡ attractors of network dynamics



Hopfield Model: An Attractor Network Model for Associative Memory

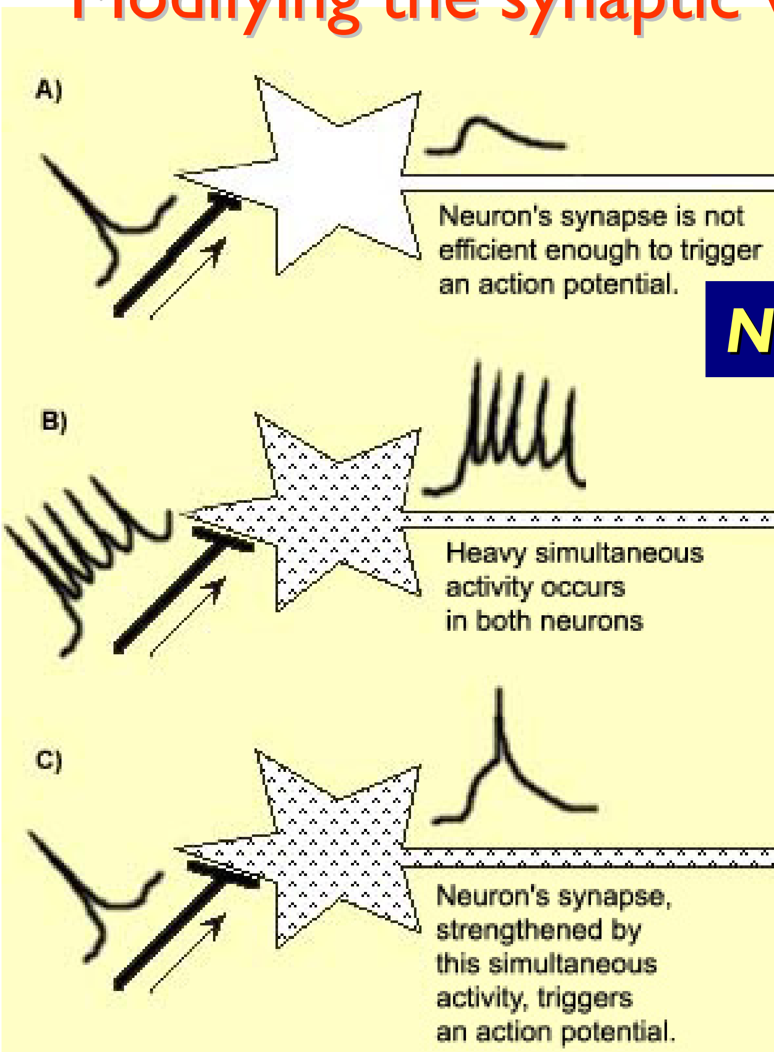
Hopfield and Tank, PNAS, 1982.

- Network of inter-connected binary state "neurons"
- x_i ={-1 or OFF,+1 or ON}.
- Activation of the neurons are defined by $x_i = \mathrm{sgn}(\sum_j w_{ji} x_j)$
  - Sgn (q) = –1, if q < 0; = +1 otherwise
  - T=0 or deterministic dynamics
- Symmetric connection weights,
  - i.e. $w_{ij} = w_{ji}$
- w_{ii}=0 (No self connections)

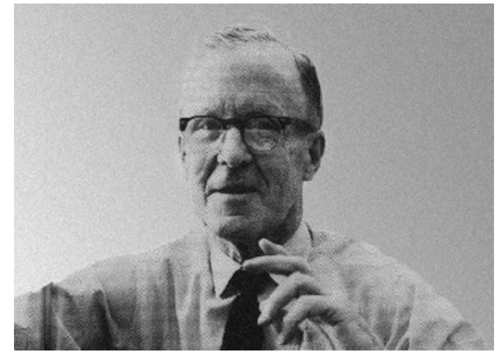


Learning

Modifying the synaptic weights by Hebb rule



http://thebrain.mcgill.ca



Donald O Hebb (1904-85)

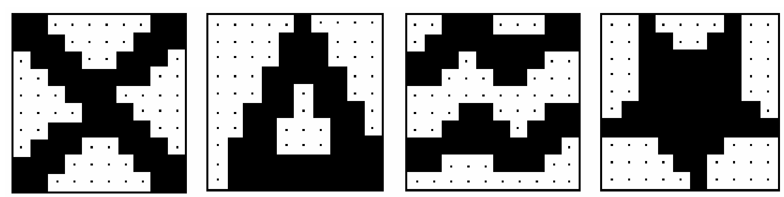
Hebb's hypothesis (1949)

Neurons that fire together, wire together

$$w_{ij} = \frac{1}{N}\sum_{p=1}^{M} \xi_i^p \xi_j^p$$

ξ_i^p: i^{th} component of the p^{th} binary pattern

Four stored patterns in simulation



"■" i^{th} neuron is excited $x_i=1$

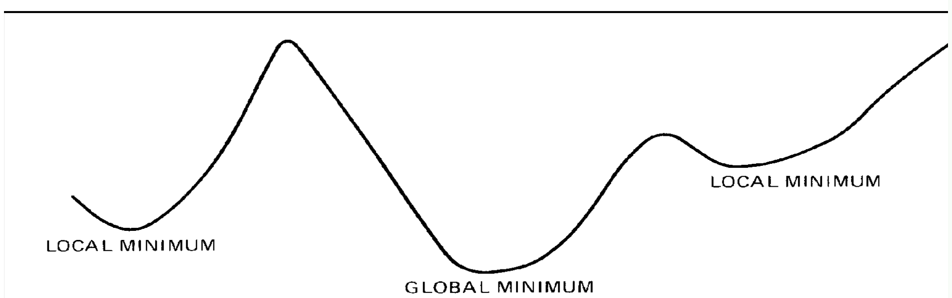
"." i^{th} neuron is resting $x_i=0$

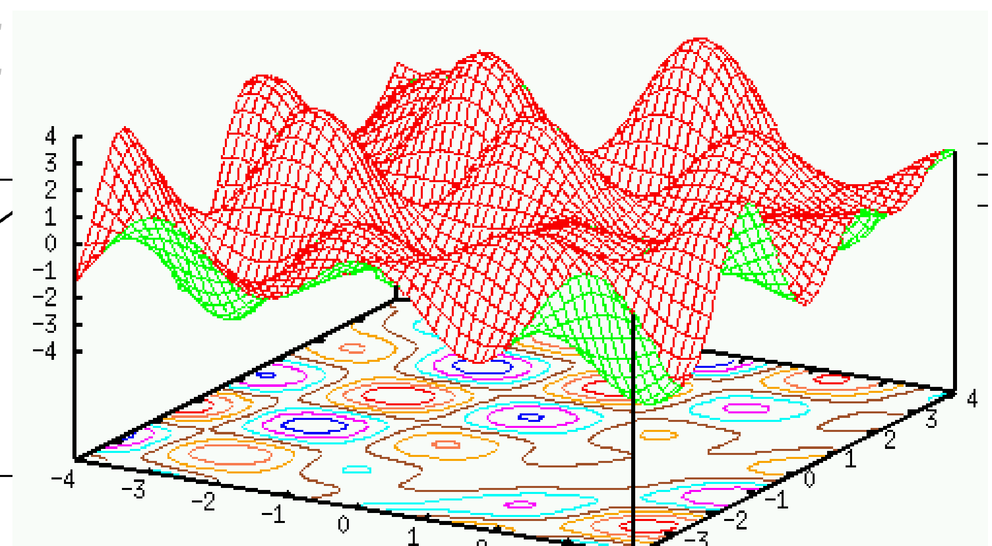
Recall dynamics of Hopfield Network

- Start from arbitrary initial configuration of {x}
- What final state does the network converge ?
- Evaluate an 'energy' value associated with the network state:

$$E = -\frac{1}{2}\sum_{j}\sum_{\substack{i=1\\ i\neq j}}^{N} w_{j,i}x_i\ x_j$$

- System converges to an attractor which is a local/global minimum of *E*





http://fourier.eng.hmc.edu

Consequences of meso-level structure on Dynamics

Modular structure $\Rightarrow$ robust dynamics in attractor networks

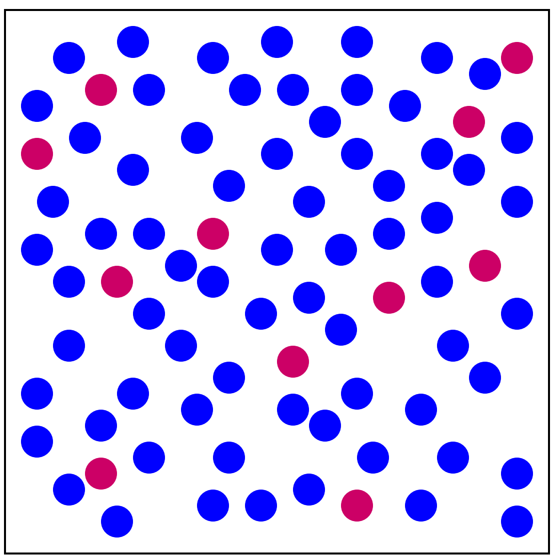
Convergence to an attractor corresponding to any of the stored patterns (recall) is most efficient when the network has an *optimal* modular structure ($r \approx r_c$)

The attractor landscape of the network changes with modularity

Isolated Modules

$r << r_c$

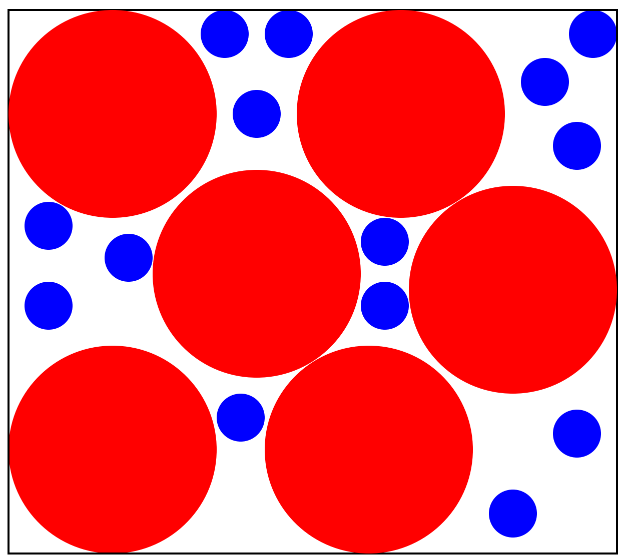
High-basin entropy



Modular

$r \approx r_c$

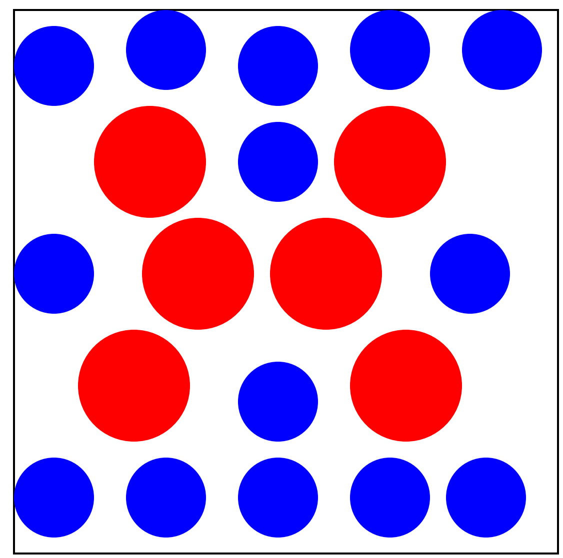
Low-basin entropy



Homogeneous

$r = 1$

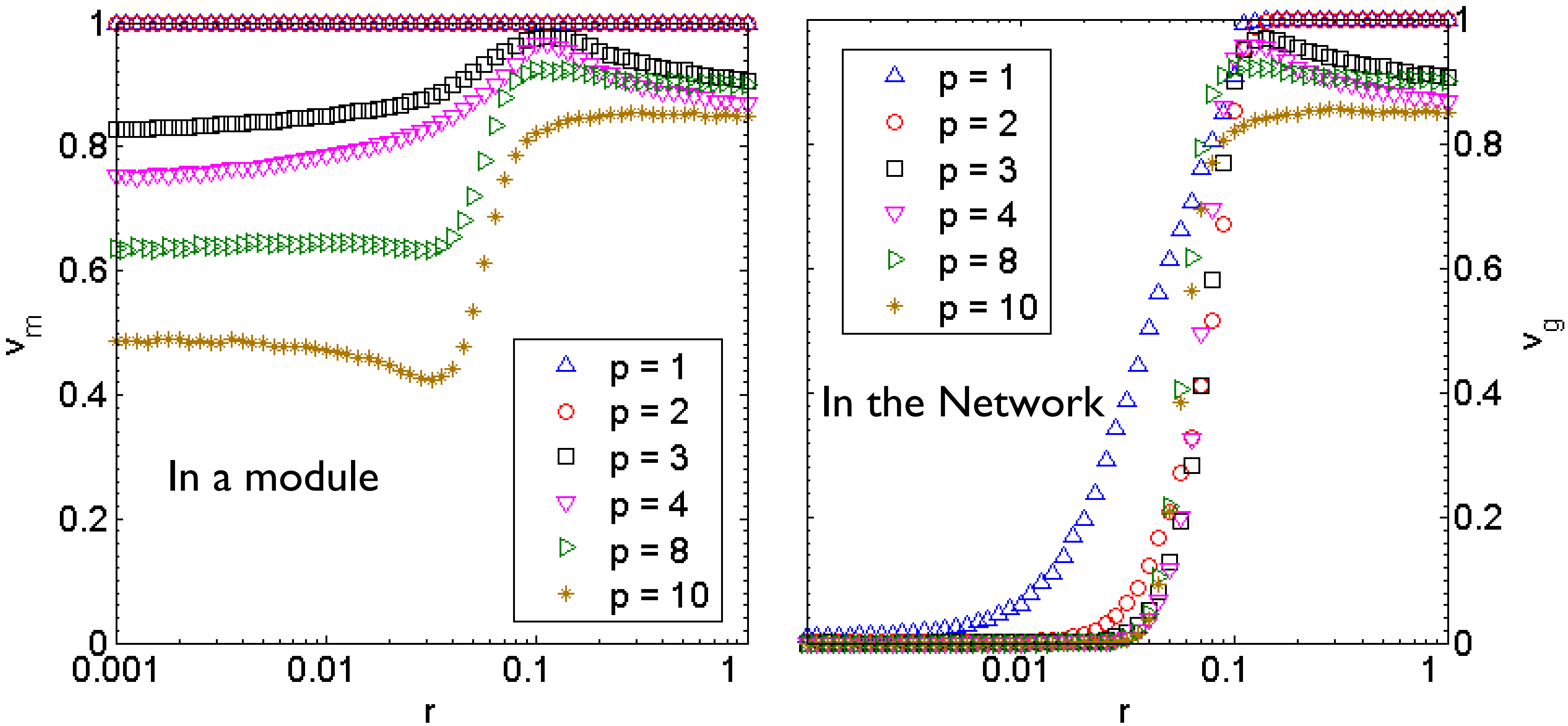
High-basin entropy



Result:

Size of basins of attraction of stored patterns, *v*…

N=1024, n=128, <k> = 120

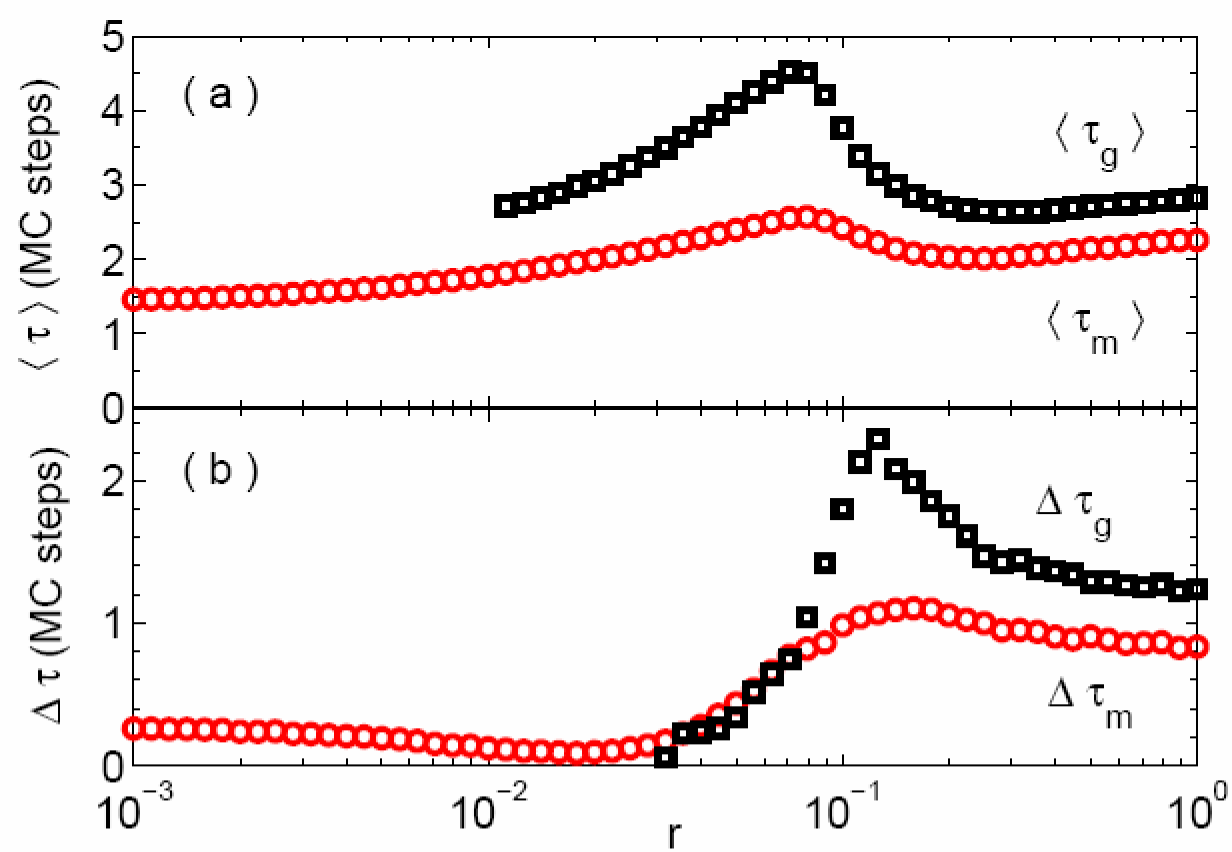


…change <u>non-monotonically</u> with modularity (*r*)

Largest at an <u>*optimal*</u> value $r_c \sim (n-1)/(N-n) \sim 0.14$

At optimal modularity, time of convergence to stored patterns faster than that to mixed states

stored patterns, $p = 4$
$N=1024$, $n=128$, $<k> = 120$



Multiple time-scales in a modular network $\Rightarrow$
Fast convergence to a stored sub-pattern within a module + slower convergence at network level

Conclusions:

- Meso-level organization – such as modularity – is ubiquitous in complex networks
- Example: C. elegans nervous system, where nodes connecting distinct modules appear to be critical for system function

- Dynamics on modular networks (but not in ER or WS networks) show distinct, separate time-scales
- manifested as Laplacian spectral gap seen in real networks (e.g., cortico-cortical brain networks)

- Modular organization may arise through multi-constraint optimization
- Advantageous for global stability of network dynamical attractors

Thanks

Work done in collaboration with

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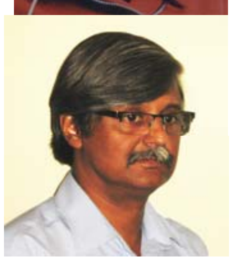

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