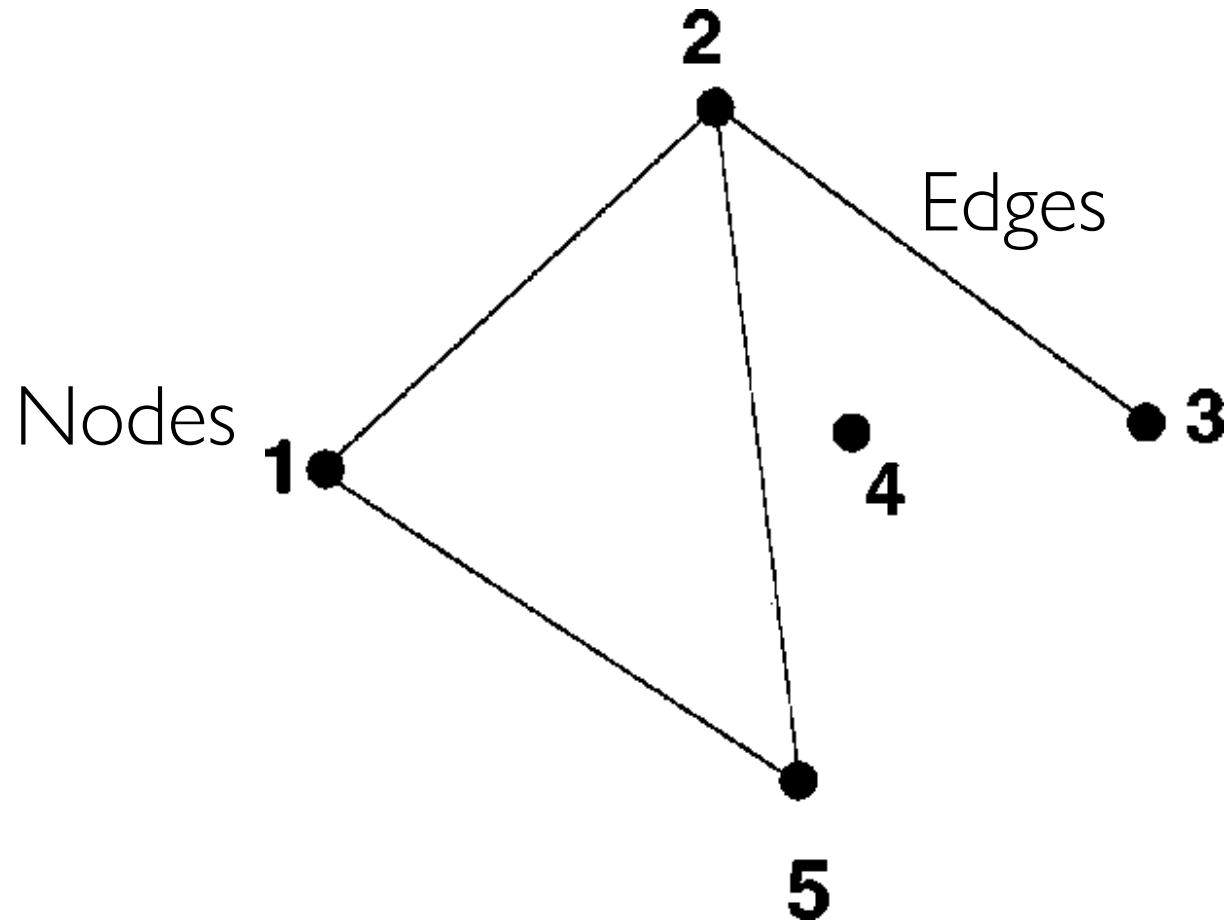


Graph Theory and Connectivity

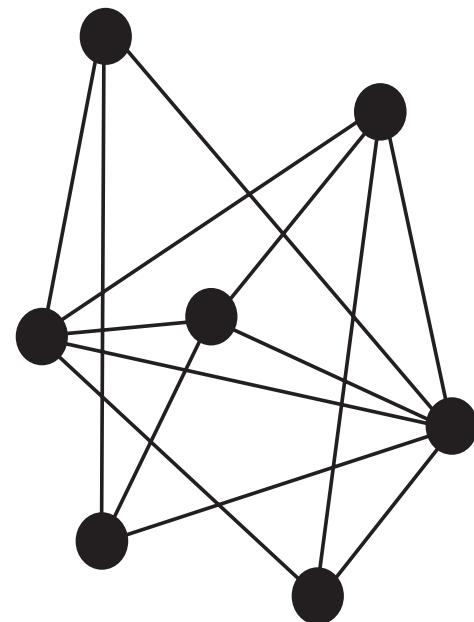


What is a graph?

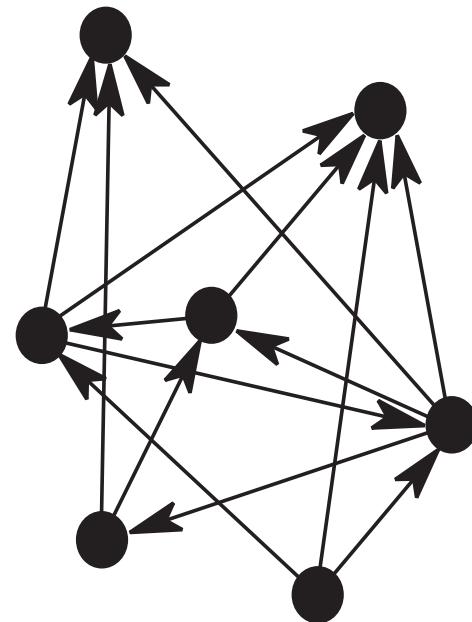




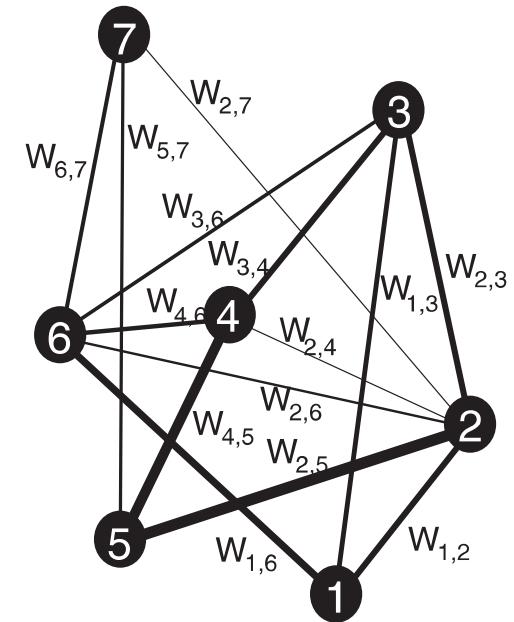
Different types of graphs



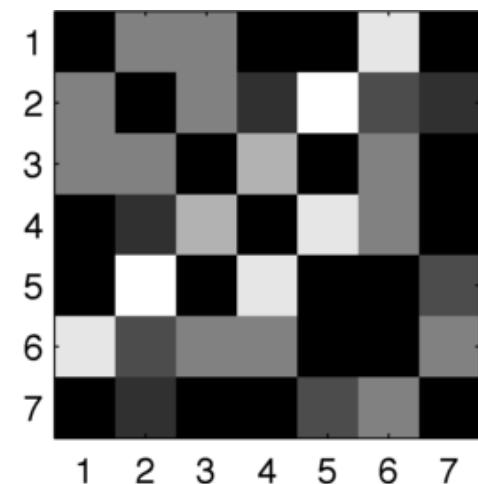
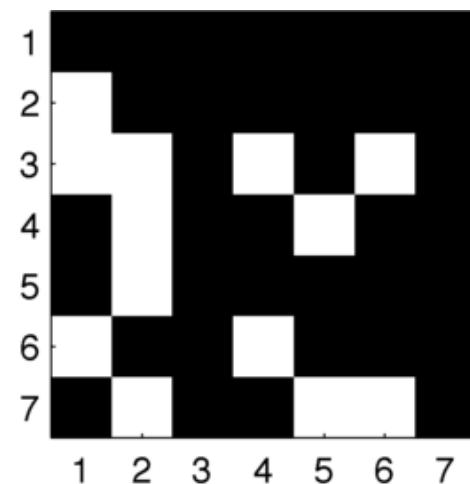
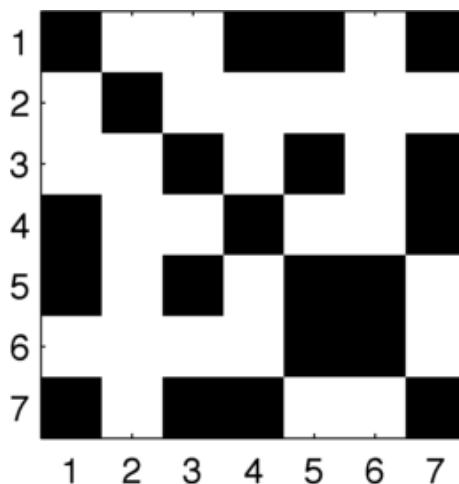
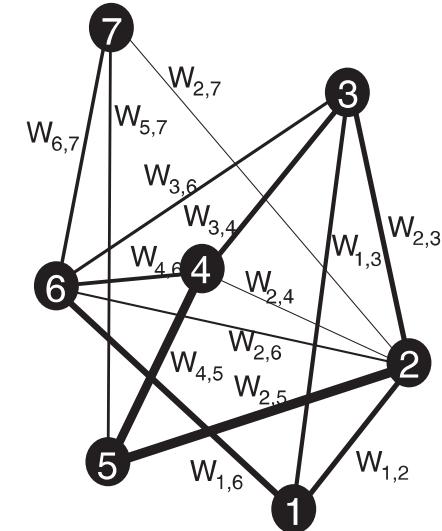
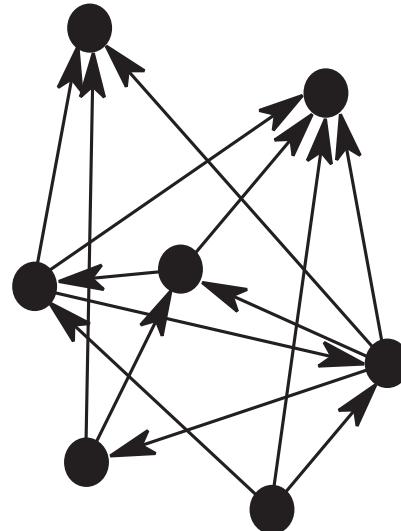
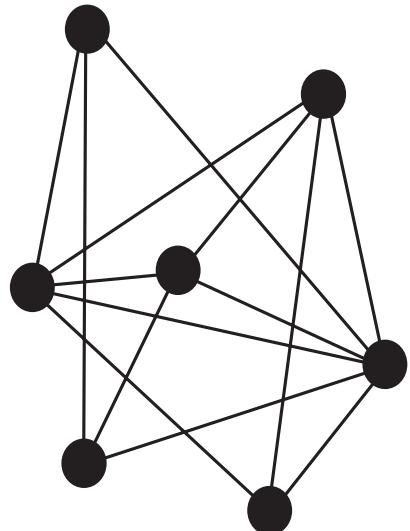
Directed



Weighted



Matrix Form





Why do we care about graphs?

- Our neuroscientist half:
 - Assess connections among networks of neurons
- Our computational half:
 - Visualize and solve difficult computational problems
- Focus of today will be on the former



Neurons are Connected

- We know how to characterize neural responses in isolation
 - STA
 - Information Theory
 - “Noise Correlations”



Neurons are Connected

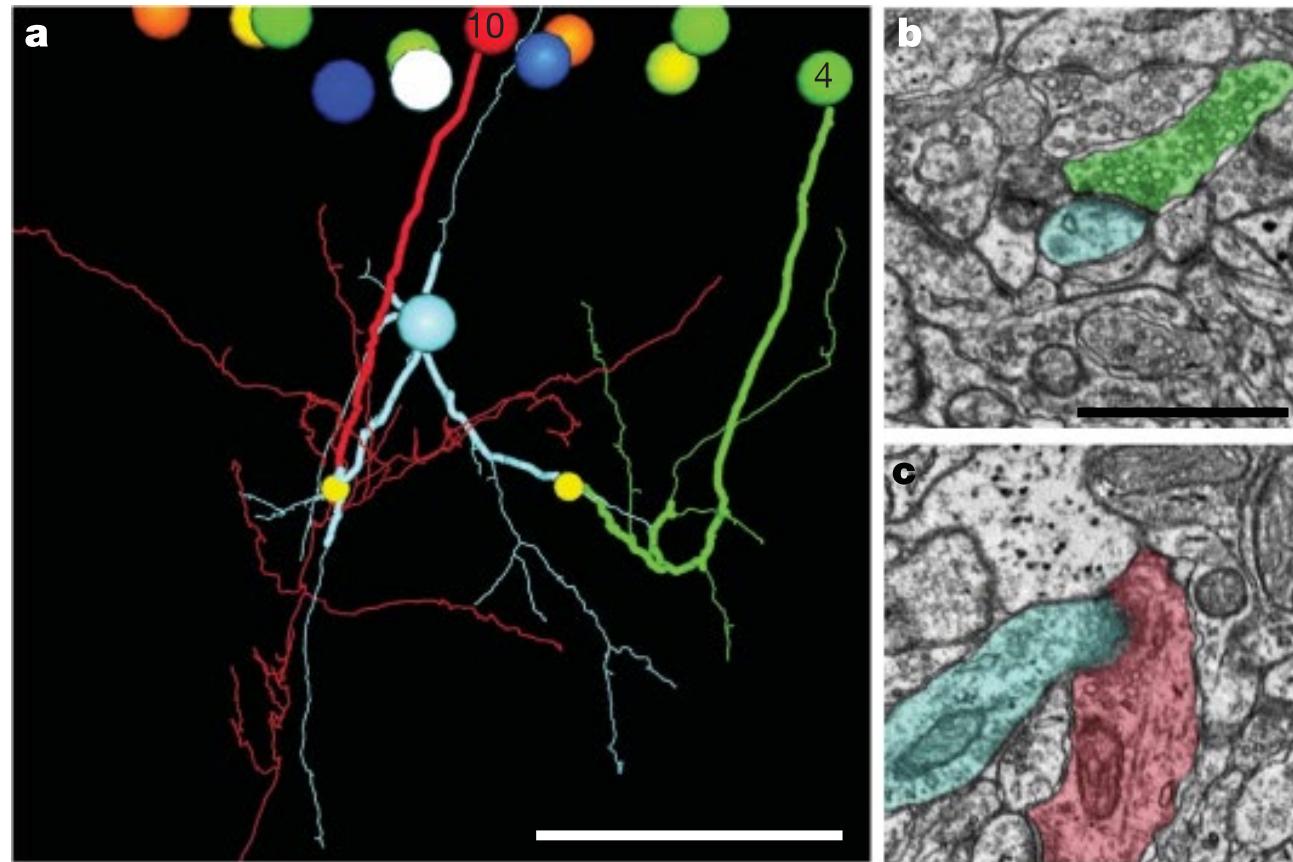
- Neurons are not isolated
- Neurons are connected
- Neural connections are probably functionally important



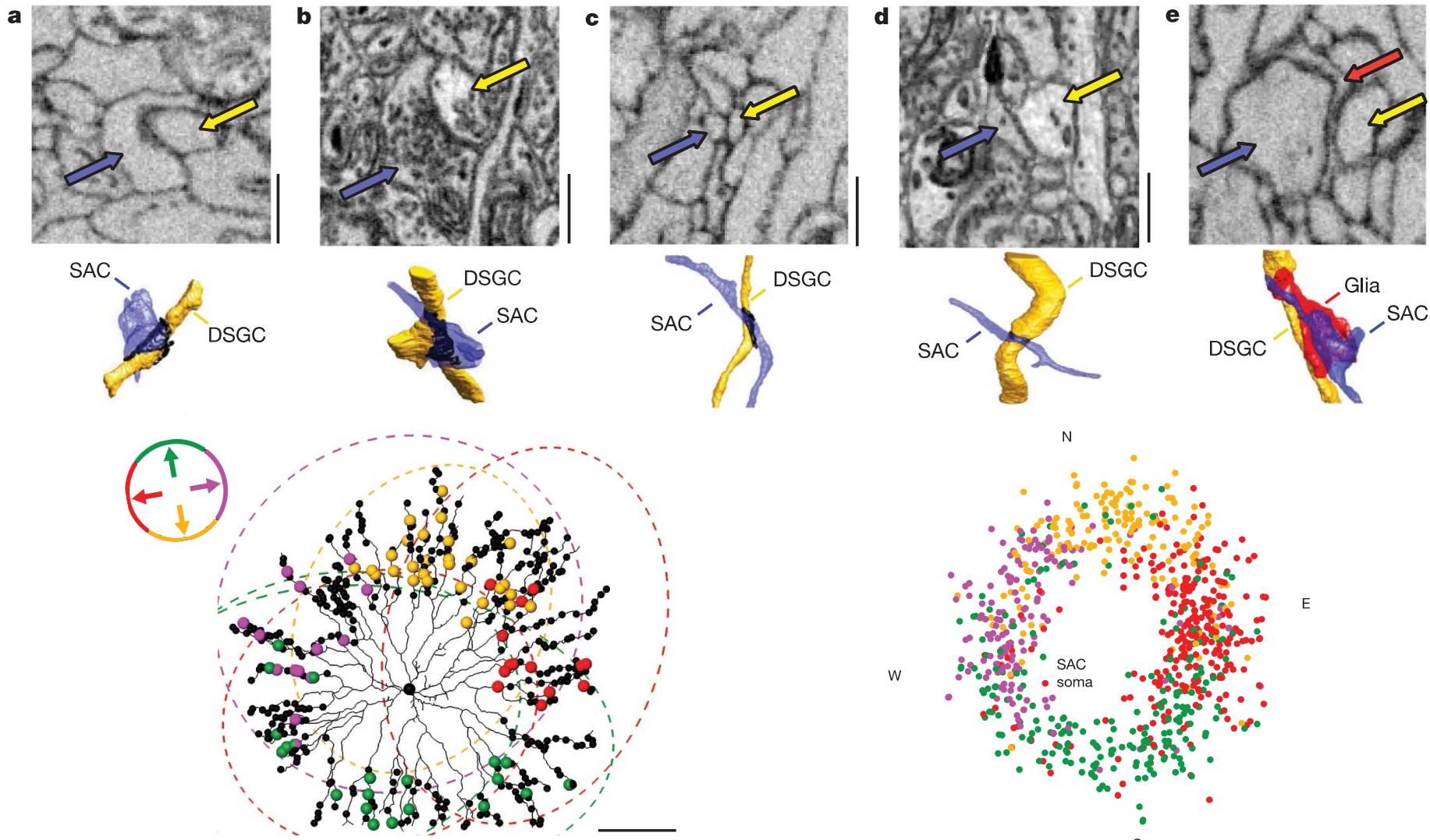
Neurons are Connected

- How to measure neural connectivity?
 - Anatomical Connectivity
 - Effective Connectivity
 - Functional Connectivity

Anatomical Connectivity



Anatomical Connectivity



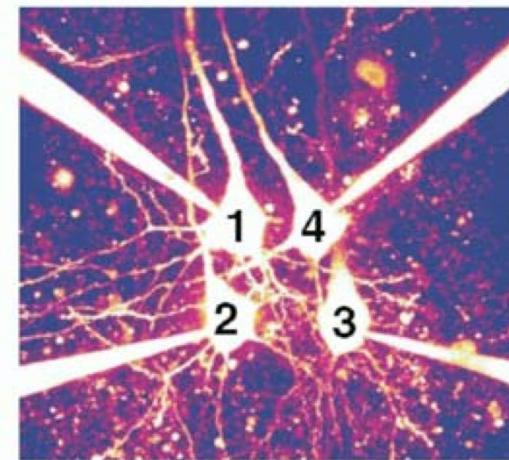
Briggman et al. 2011

Effective Connectivity

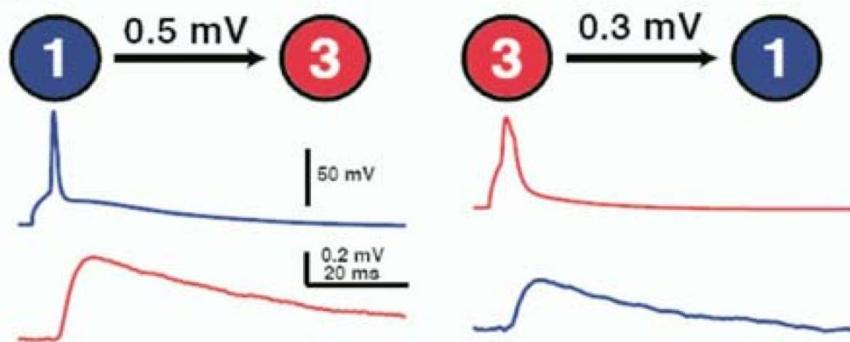
A



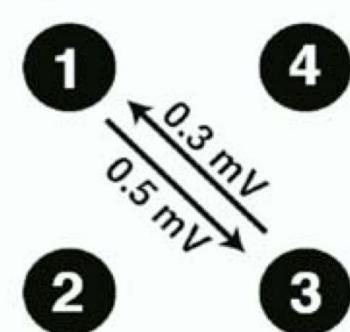
B



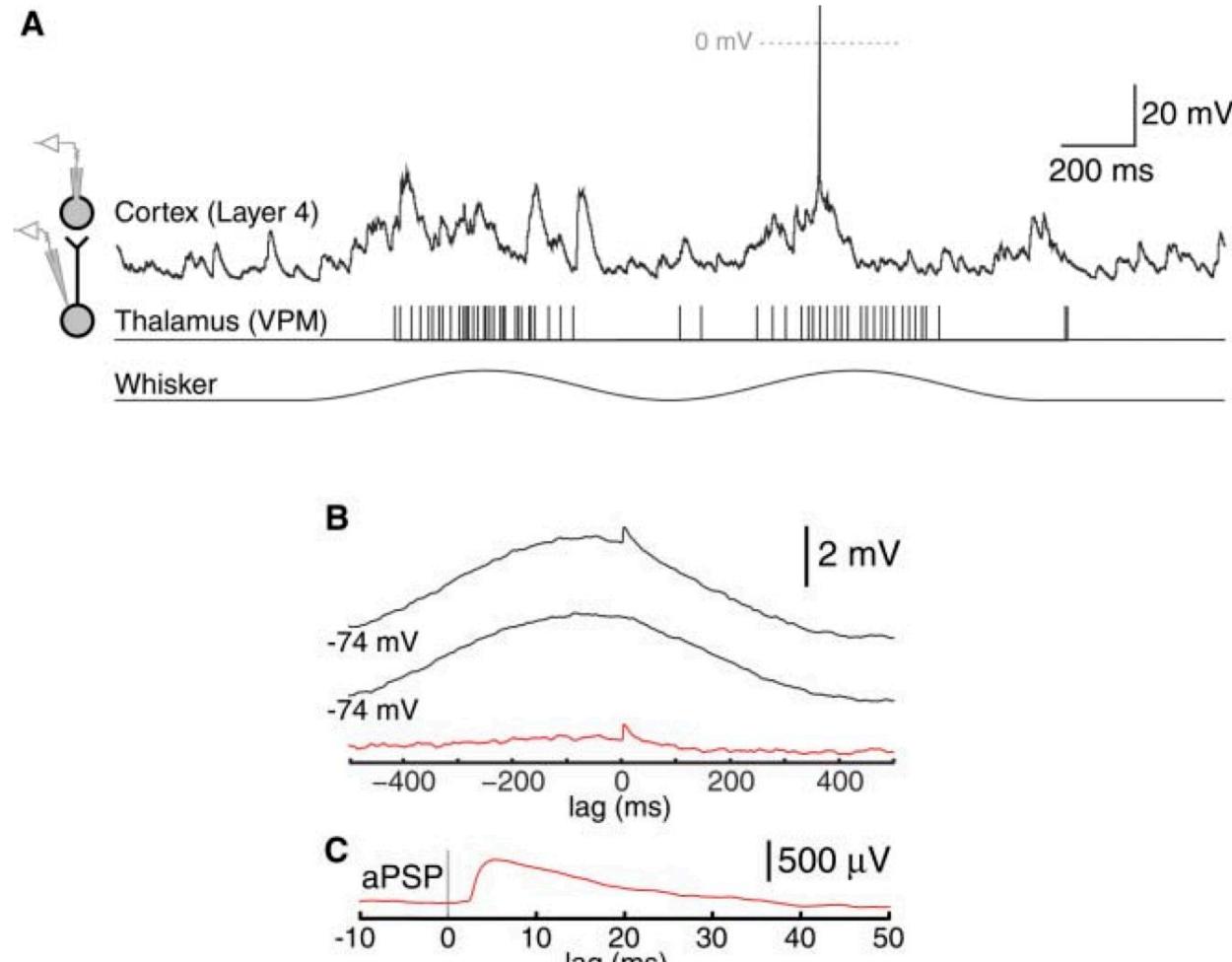
C



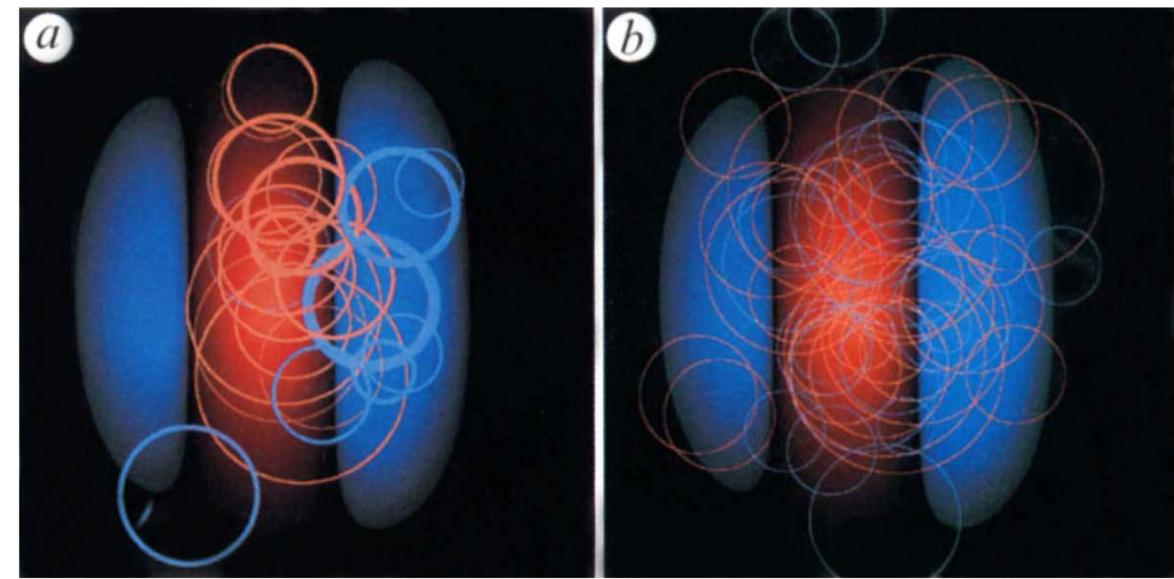
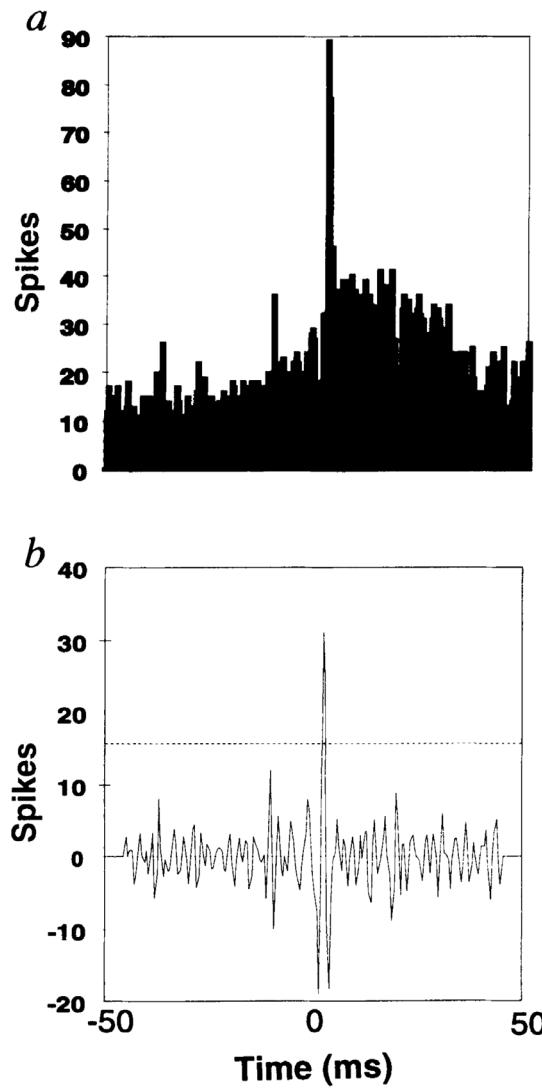
D



Effective/Functional Connectivity



Functional Connectivity

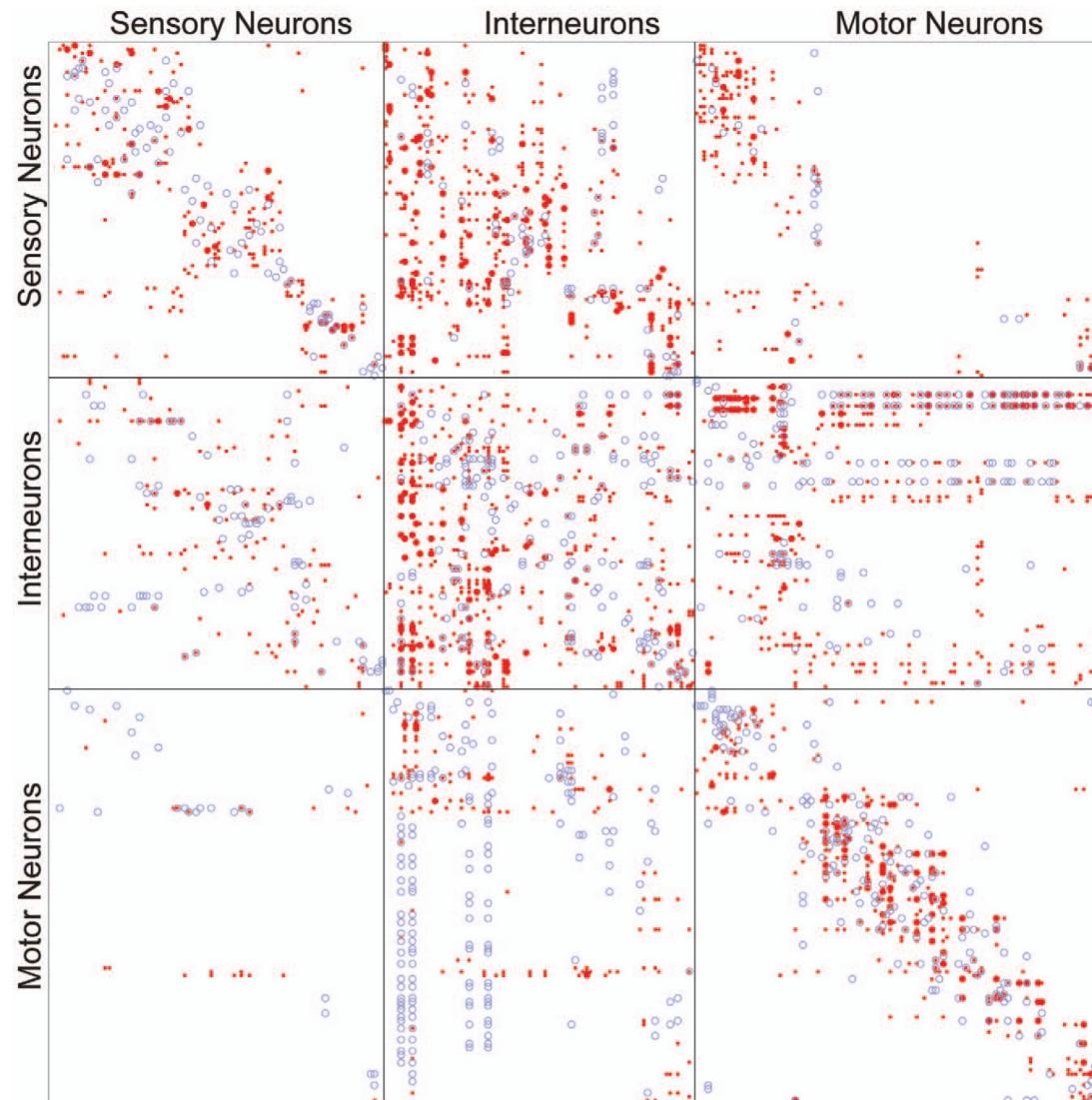


Reid and Alonso 1995

Now what?

- Consider neurons as nodes and synapses as edges
- Connectivity measures dictate edge
 - Locations
 - Directedness
 - Weights

C elegans adjacency matrix



Now what?

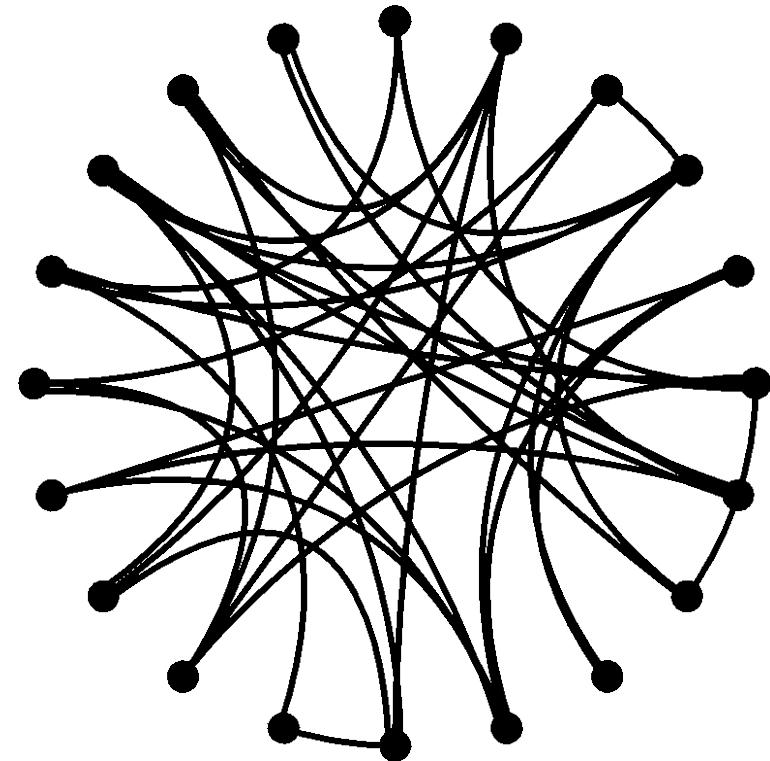
- We need priors to make interpretations of our graphs meaningful
- We need summary measures to describe big networks in the first place

Graph Priors

- Random (Erdős–Rényi) Graphs
- Regular Graphs
- Small-World Graphs

Random Graphs

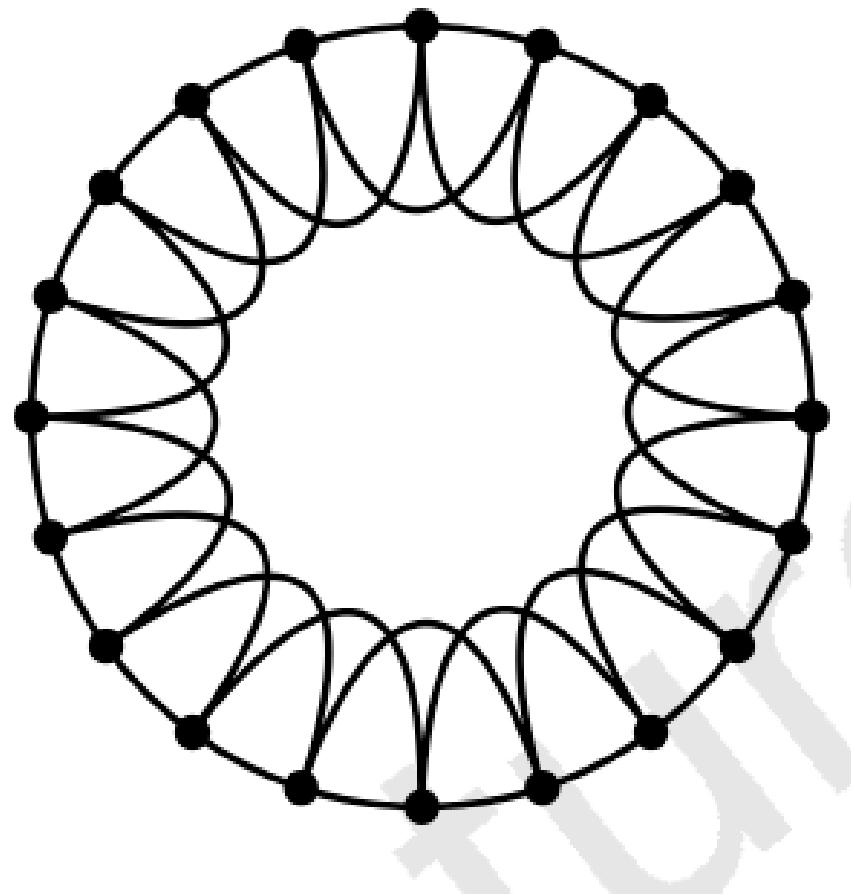
- Defined by a uniform, independent connection probability between any two nodes



Watts and Strogatz 1996

Regular Graphs

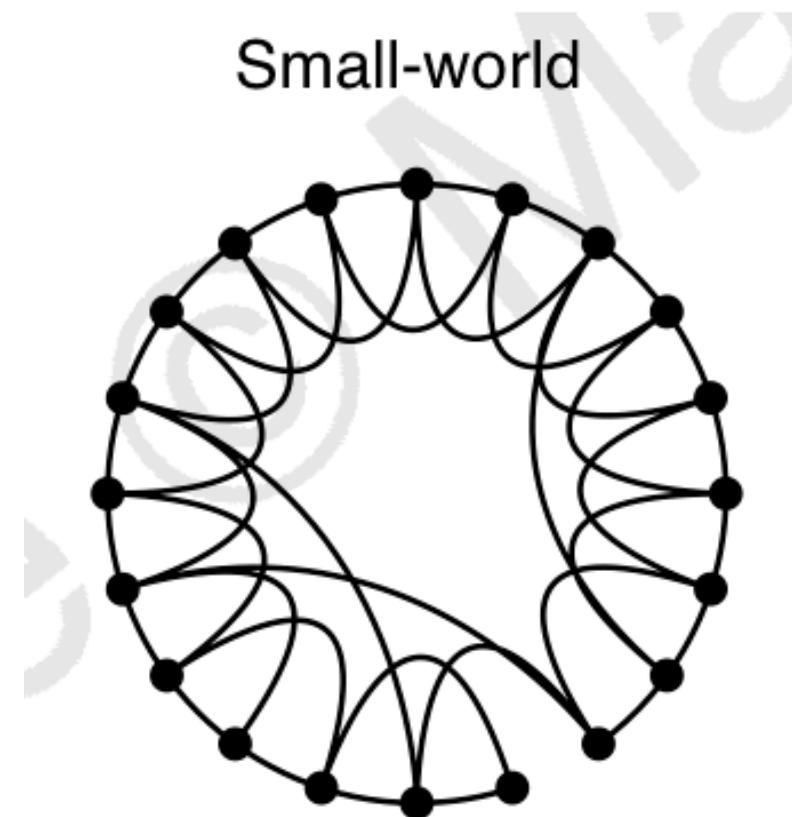
- Deterministic edge distributions
- Often determined by Euclidian distance



Watts and Strogatz 1996

Small-World Graphs

- Generate regular graph
- Randomly shuffle edge connections from a subset of nodes
- Determined by uniform shuffling probability



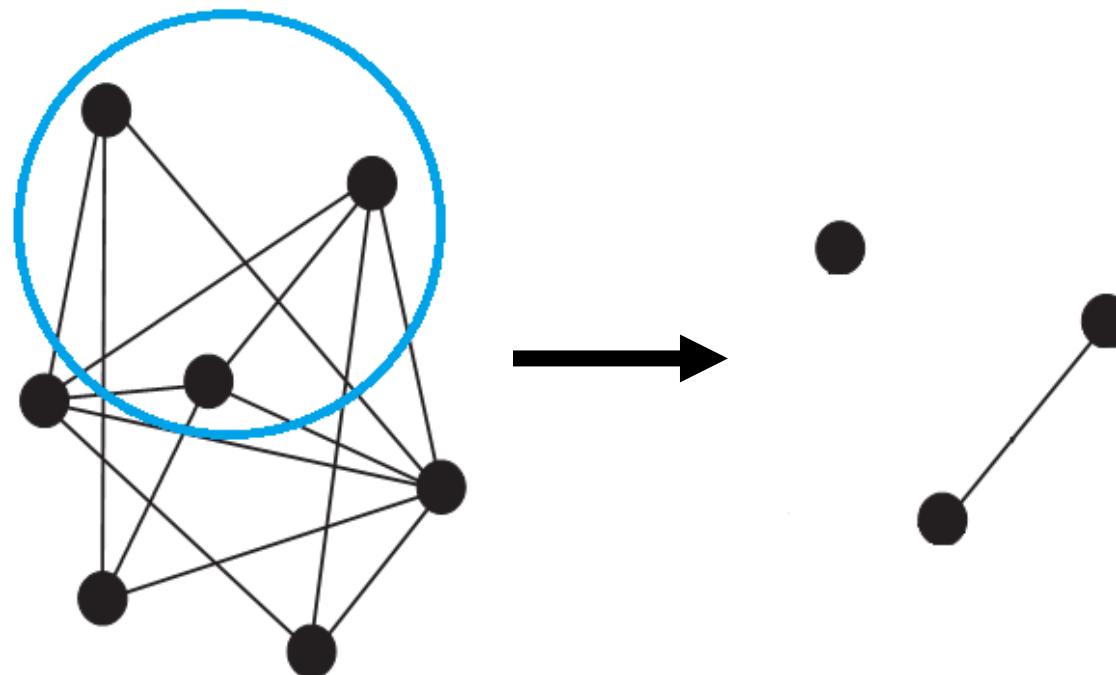
Watts and Strogatz 1996

Graph measures

- Motif frequencies
- Clustering coefficient
- Characteristic path length
- Degree distribution

Motif Frequencies

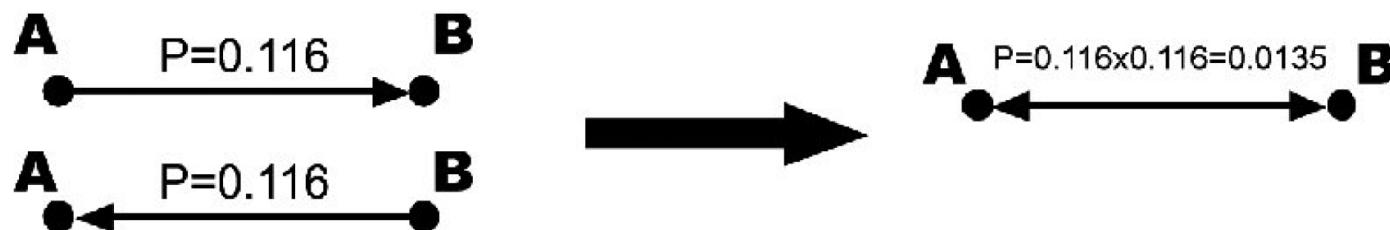
- *Subgraph*: A subset of nodes & their connected edges lifted from a larger graph



Motif Frequencies

- Analyze the likelihood of all possible N-sized subgraphs
- Usually compared against random priors

Null hypothesis assumes independent connection probabilities

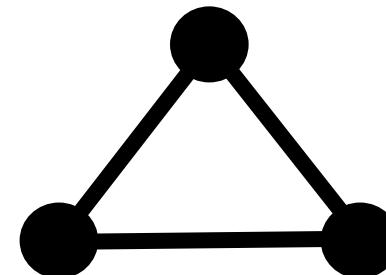


Motifs: Random Prior

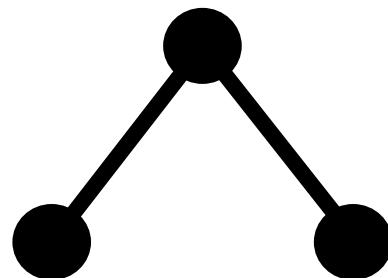
For simple, undirected, unweighted random graphs with connection probability p :



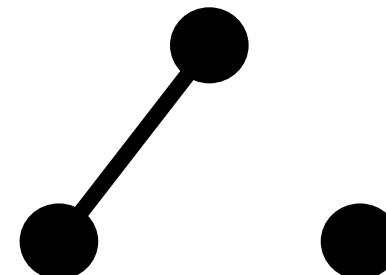
$$P(\text{edges}|\text{subgraph}) = p$$



$$P(\text{edges}|\text{subgraph}) = p^3$$



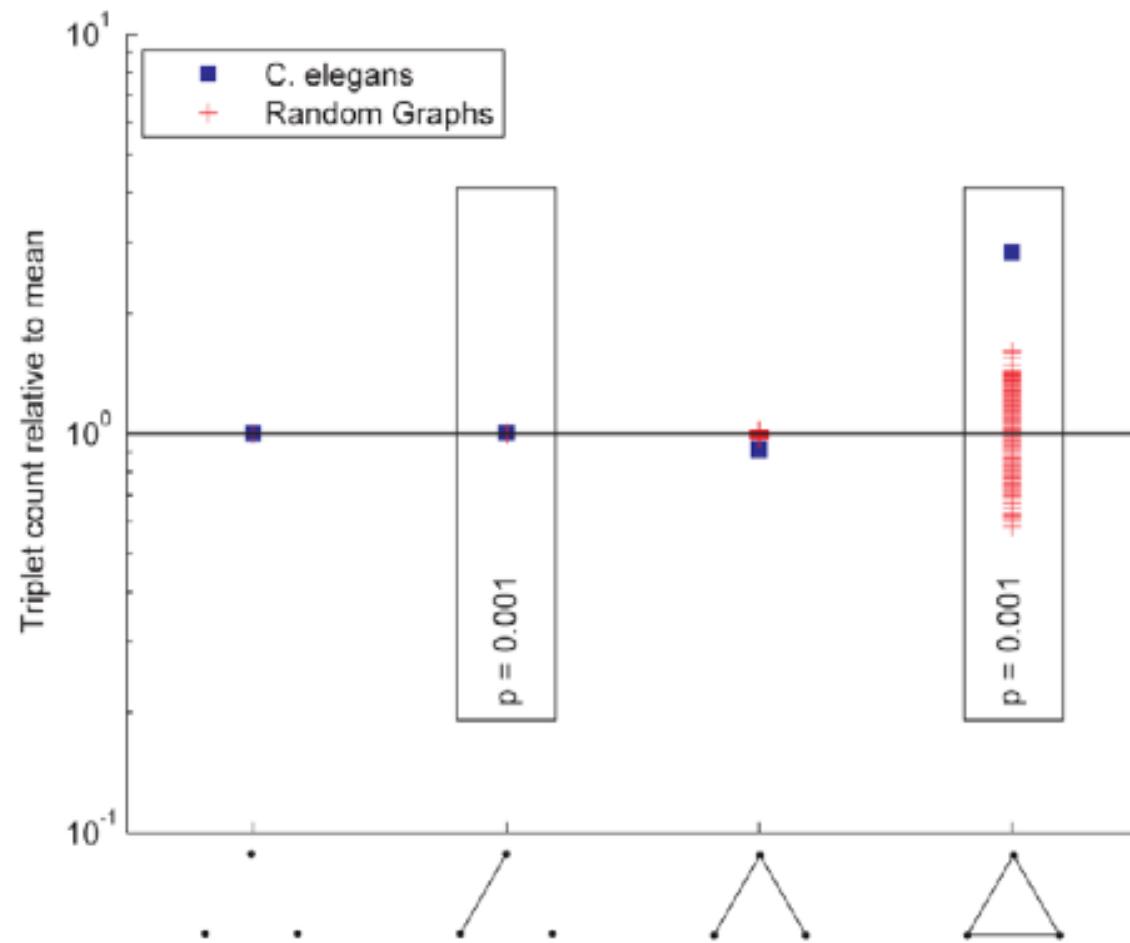
$$P(\text{edges}|\text{subgraph}) = C_2^3 p^2 (1 - p)$$



$$P(\text{edges}|\text{subgraph}) = C_1^3 p (1 - p)^2$$



Motifs: *C elegans* vs. Random



Clustering Coefficient

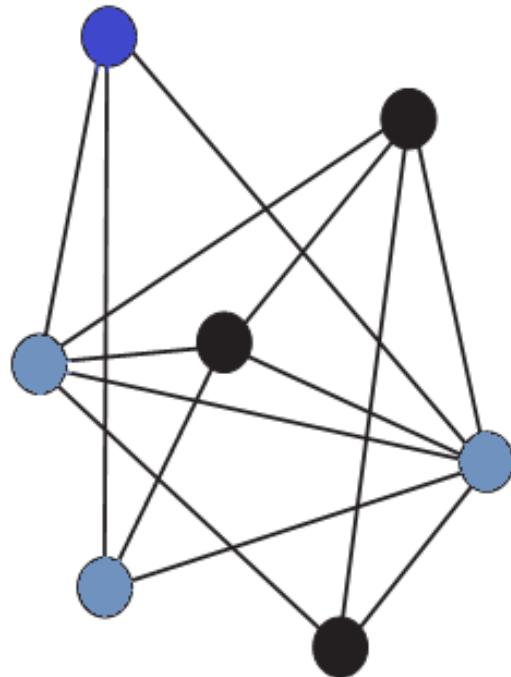
- *Complete Graph:* A graph of N nodes in which each node is connected to all other nodes in the network
- Complete subgraphs known as “cliques”
- For a simple, unweighted, undirected network:

$E \equiv$ number of edges

$$E = \frac{1}{2}N(N - 1)$$

Clustering Coefficient

- *Neighborhood:* For some node, the subgraph of all nodes connected to it.

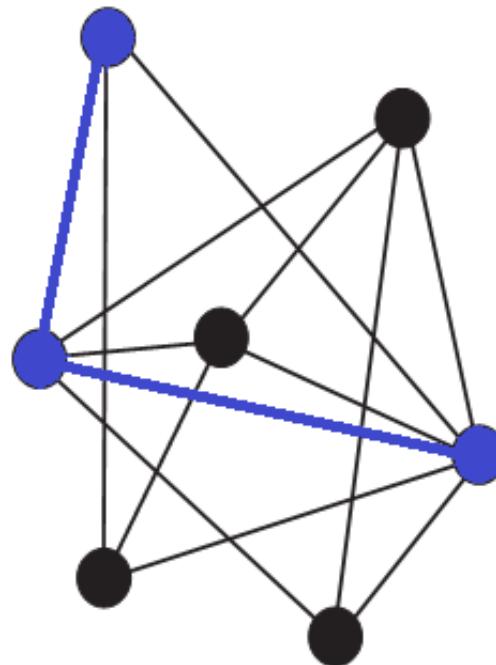


Clustering Coefficient

- Two types: local and average
 - Local: Completeness (clique-ness) of the neighborhood of node i
 - For a neighborhood with n_i nodes and adjacency matrix with binary elements of the type c_{jk} :
$$C_i = \frac{\sum_{j < k} c_{jk}}{\frac{1}{2} n_i (n_i - 1)}$$
 - Average: Mean clustering across all N nodes of the full graph:
$$\langle C \rangle = \frac{1}{N} \sum_{i=1}^N C_i$$

Characteristic Path Length

- *Path*: Alternating sequence of edges and nodes, beginning and terminating with a node
- *Path Length*: Sum of edge weights in a path





Characteristic Path Length

- *Minimum Path Length:* For a given pair of nodes, the minimum edge count among all possible paths
- Solved using Dijkstra's algorithm

Minimum Path Length Solution

```
function Li = Dijkstra(A,i)
% Takes adjacency matrix A, starting node index i
% mark non-existent edges as having weights of inf
% Li gives the minimum distance to each node
% for directed graphs, columns dictate the "from" node

n          = size(A,1);           % node count
Li         = inf(n,1);           % distance functions initialized to inf
Li(i)      = 0;                  % starting point w/0 dist by definition
uv         = 1:n;                % indices of unvisited nodes

while any(uv)
    [~,ci]    = min(Li(uv));    % find terminal index of shortest path
    current   = uv(ci);        % greedily mark as "current"
    uv(ci)    = [];             % ...and, in turn, as "visited"

    Li(uv)    = min(Li(uv),Li(current) + A(uv,current));
                           % minimum of previous distance & current
end
```

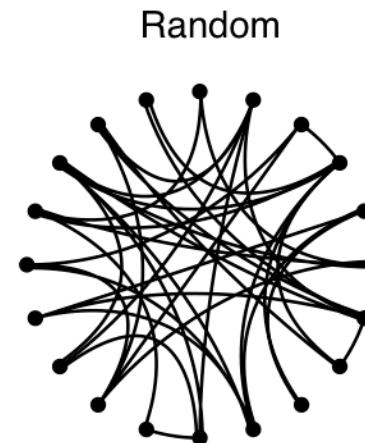
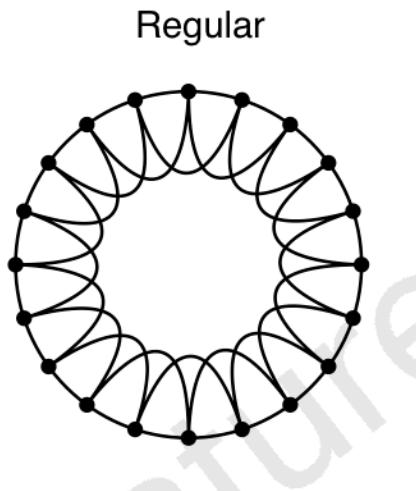
Characteristic Path Length

- *Characteristic Path Length*: The mean minimum path length across all pairs of (different) nodes:

```
>> n = size(A,1);  
>> dists = [];  
>> for i = 1:n  
    dtemp = Dijkstra(A,i);  
    dtemp(i) = [];  
    dists = vertcat(dists,dtemp);  
end  
>> mean(dists)
```

L and C of prior graphs

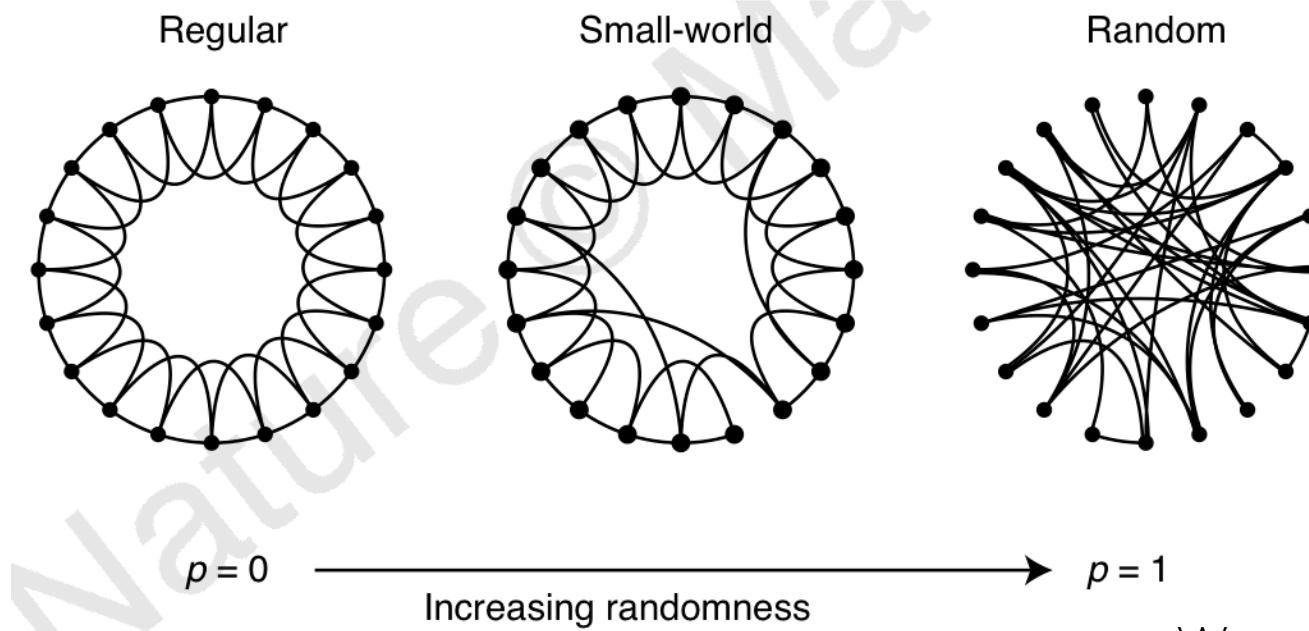
- Regular: $L \sim N$ $C \sim 1$
- Random: $L \sim \log N$ $C \sim 1/N$





L and C of prior graphs

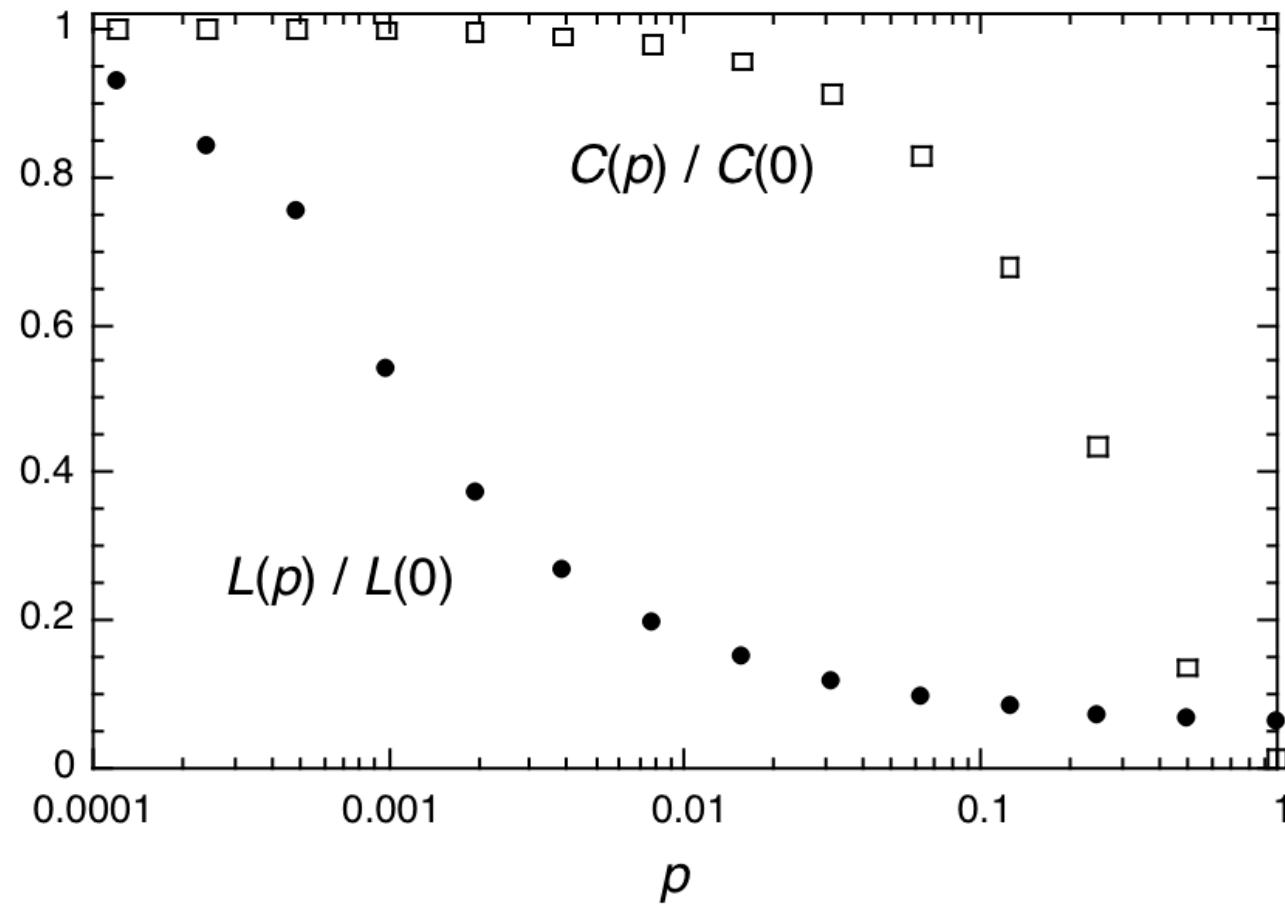
- Regular: $L \sim N$ $C \sim 1$
- Random: $L \sim \log N$ $C \sim 1/N$
- Small World: $L \sim \log N$ $C \sim 1$



Watts and Strogatz 1996



“Sweet Spot”



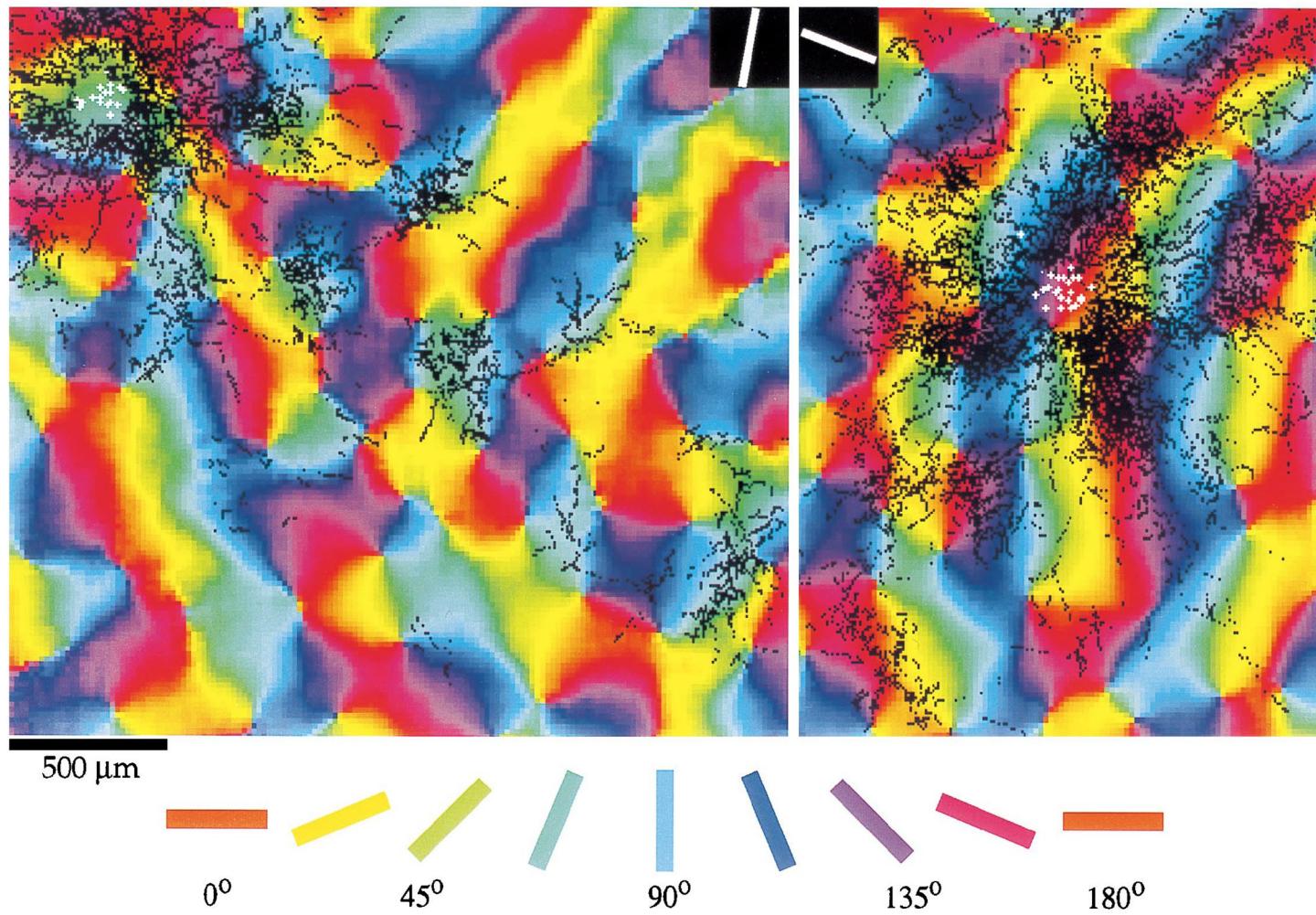
Real Networks in the “Sweet Spot”

Table 1 Empirical examples of small-world networks

	L_{actual}	L_{random}	C_{actual}	C_{random}
Film actors	3.65	2.99	0.79	0.00027
Power grid	18.7	12.4	0.080	0.005
<i>C. elegans</i>	2.65	2.25	0.28	0.05

N=279

Tree Shrew Small World

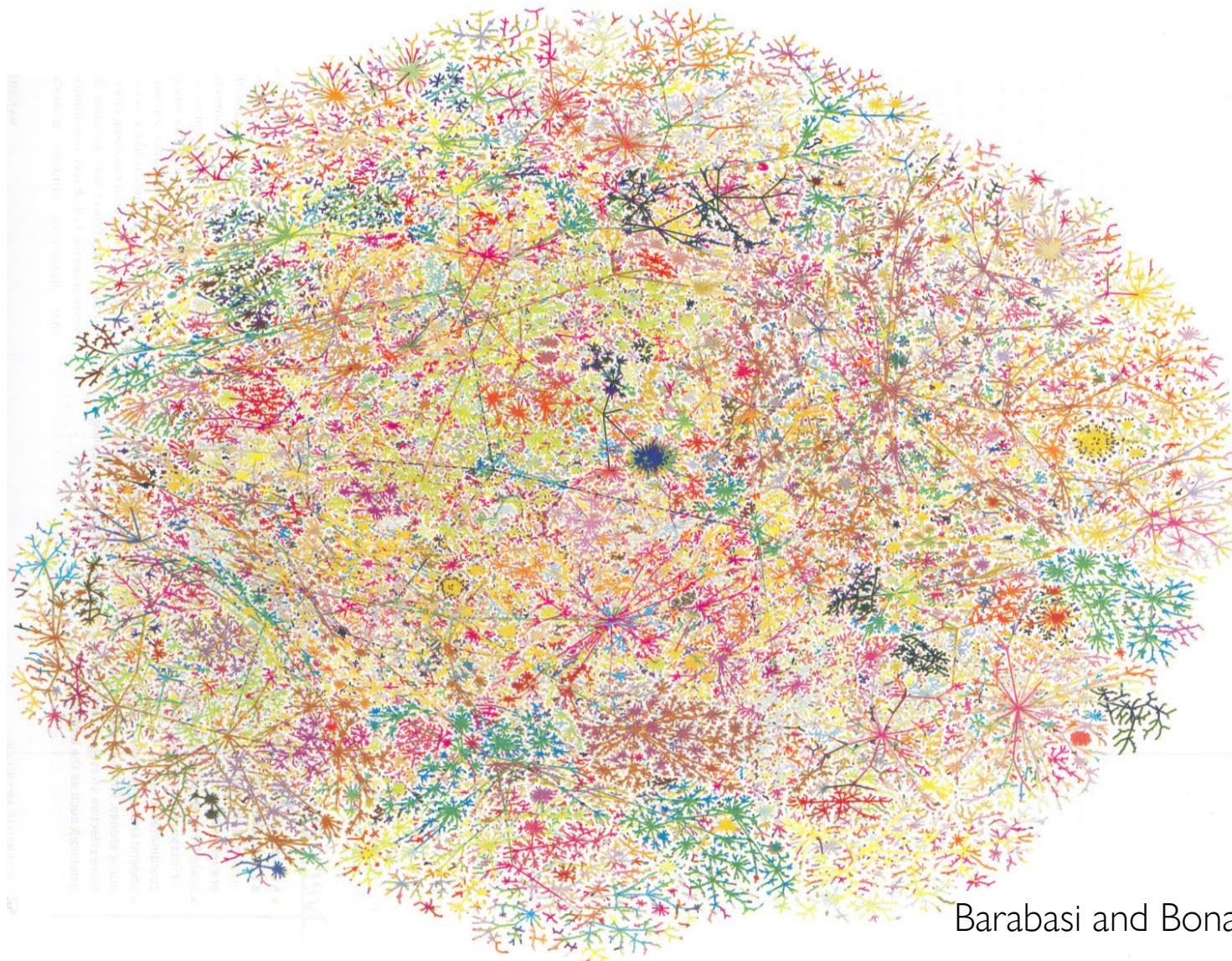


Bosking et al. 1997

Degree Distributions

- The **degree** of a node k_i is simply the number of edges connected to that node
- The **degree distribution** $P(k)$ is the probability across a network of a node having degree k .

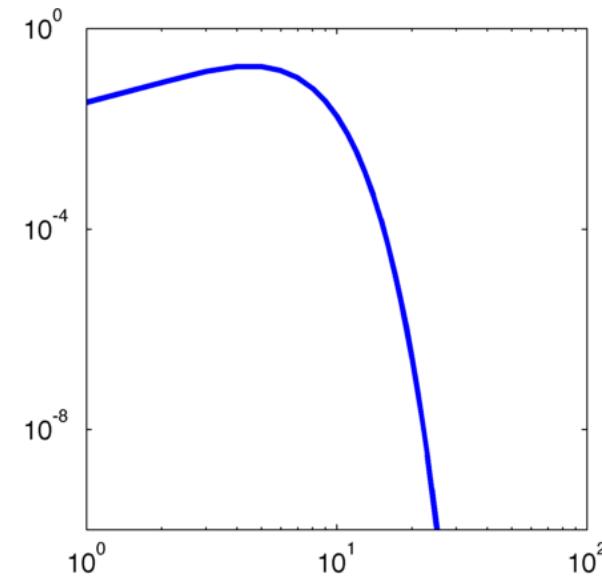
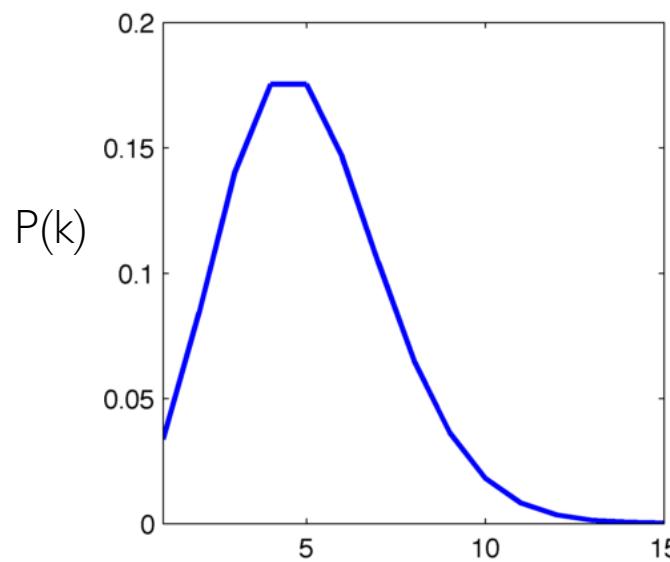
Hubs: High-Degree Nodes



Random Networks

- The degree distribution of a random network is:

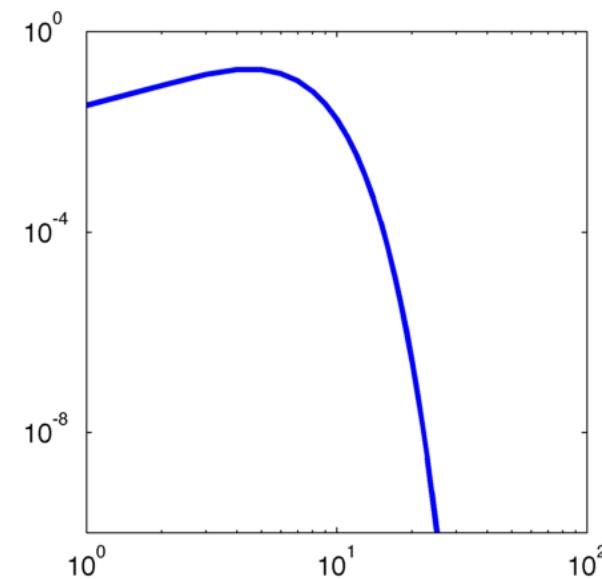
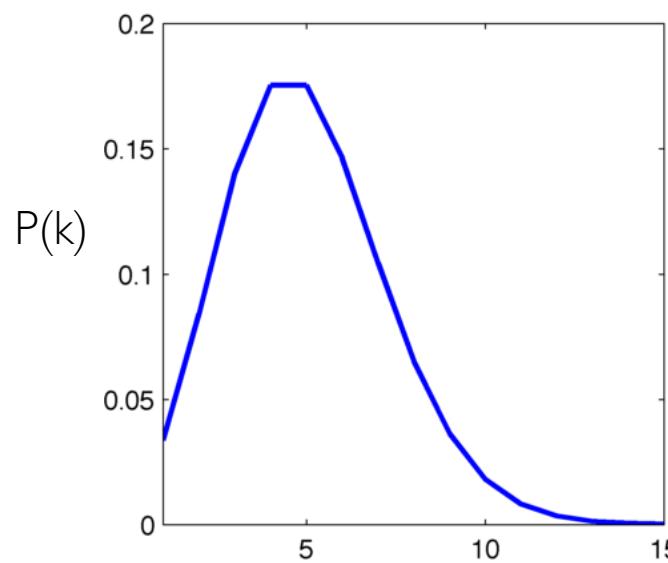
$$P(k) = \binom{N-1}{k} p^k (1-p)^{N-1-k}$$



Random Networks

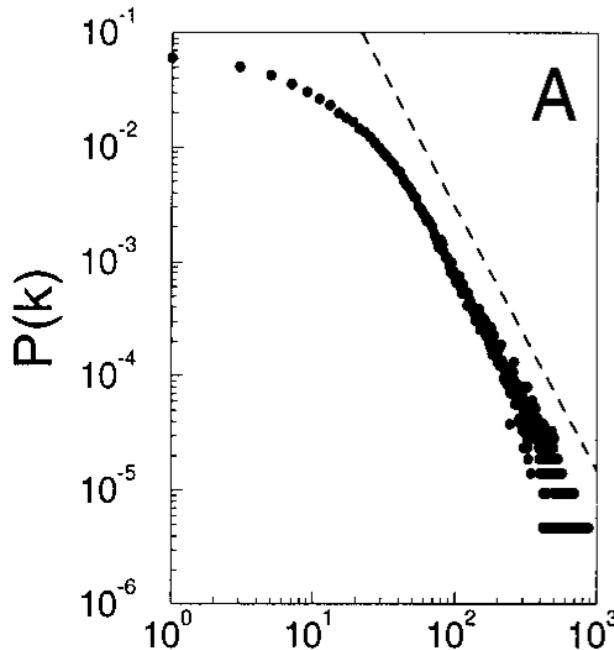
- For random networks:

- $P(k) \propto a^{-k}$

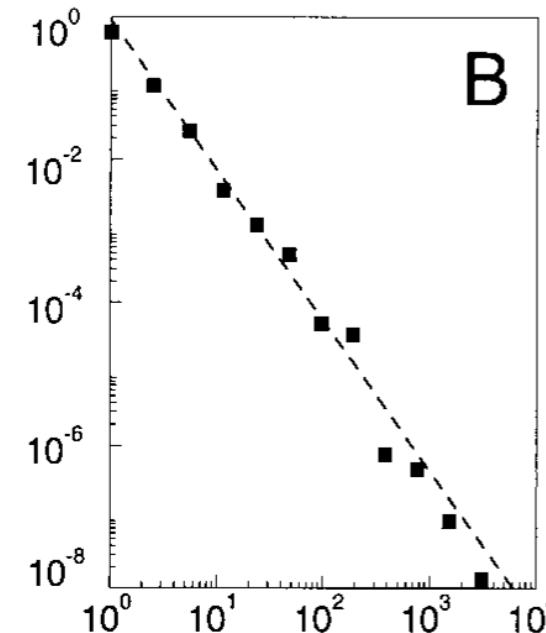


Real Networks

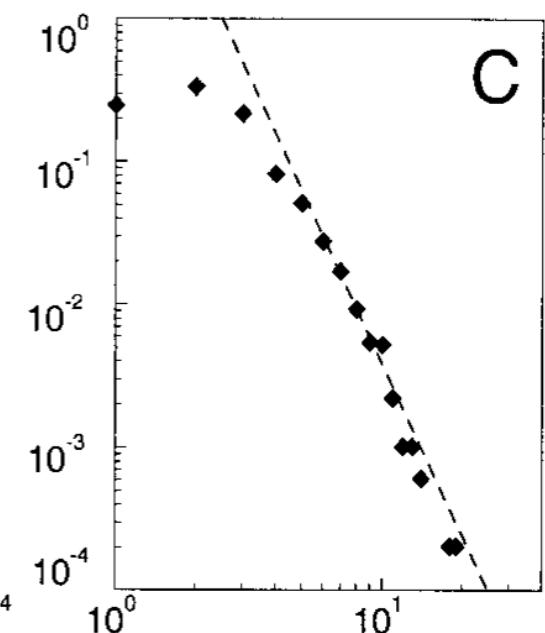
Actor Collaborations



World Wide Web



Power Grid



- Empirically, in many real networks
 - $P(k) \propto k^{-\gamma}$

Scale Invariance

- A constant scaling of the inputs leads to a constant scaling of the outputs

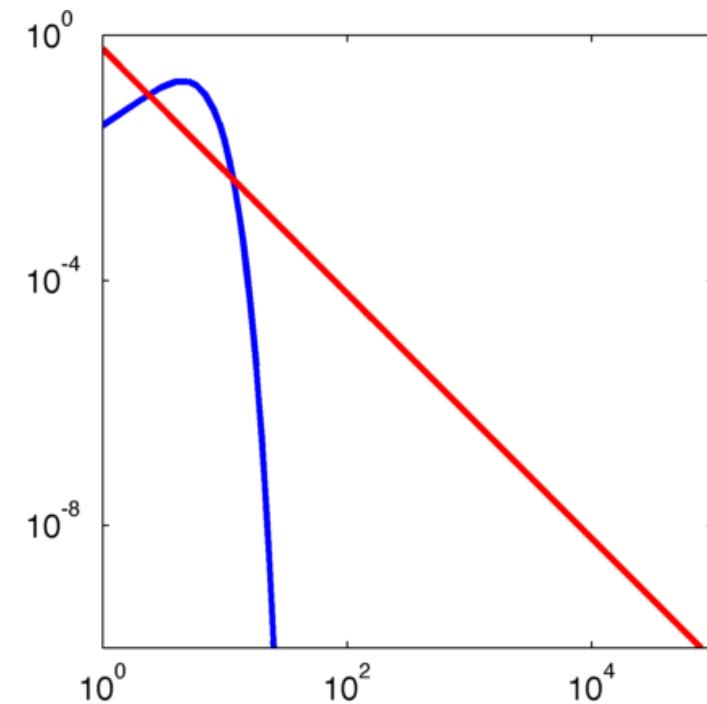
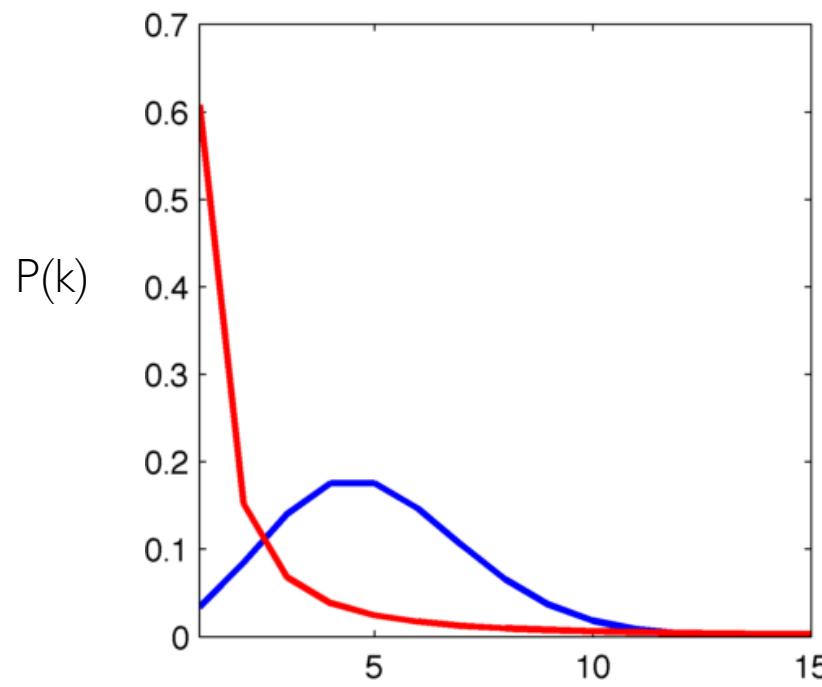
$$f(cx) = c^\gamma f(x)$$

$$f(x) = ax^\gamma$$

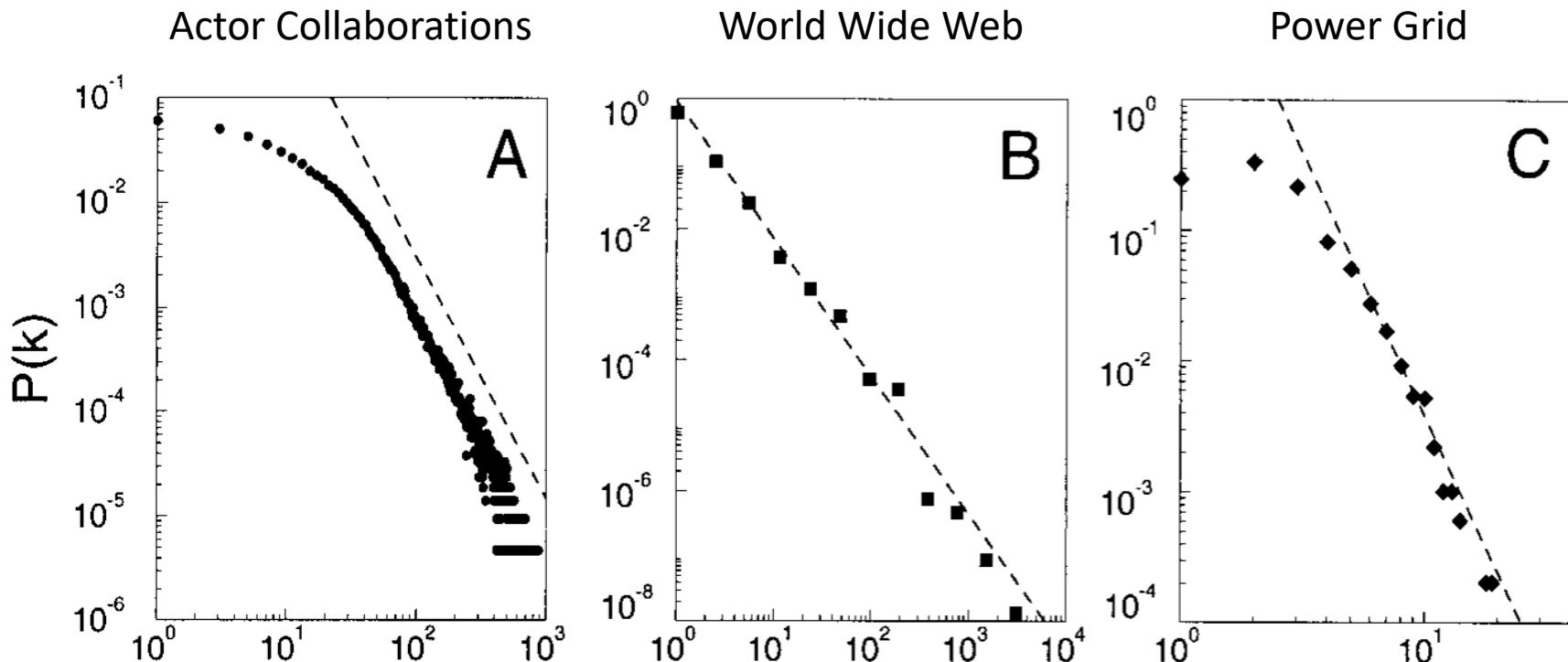
- Power laws lead to scale invariance
- A power law degree distribution defines a '*scale free*' network

Scale Free Networks

- Scale free networks have a “heavy tail”
- Thus, scale free networks have hubs



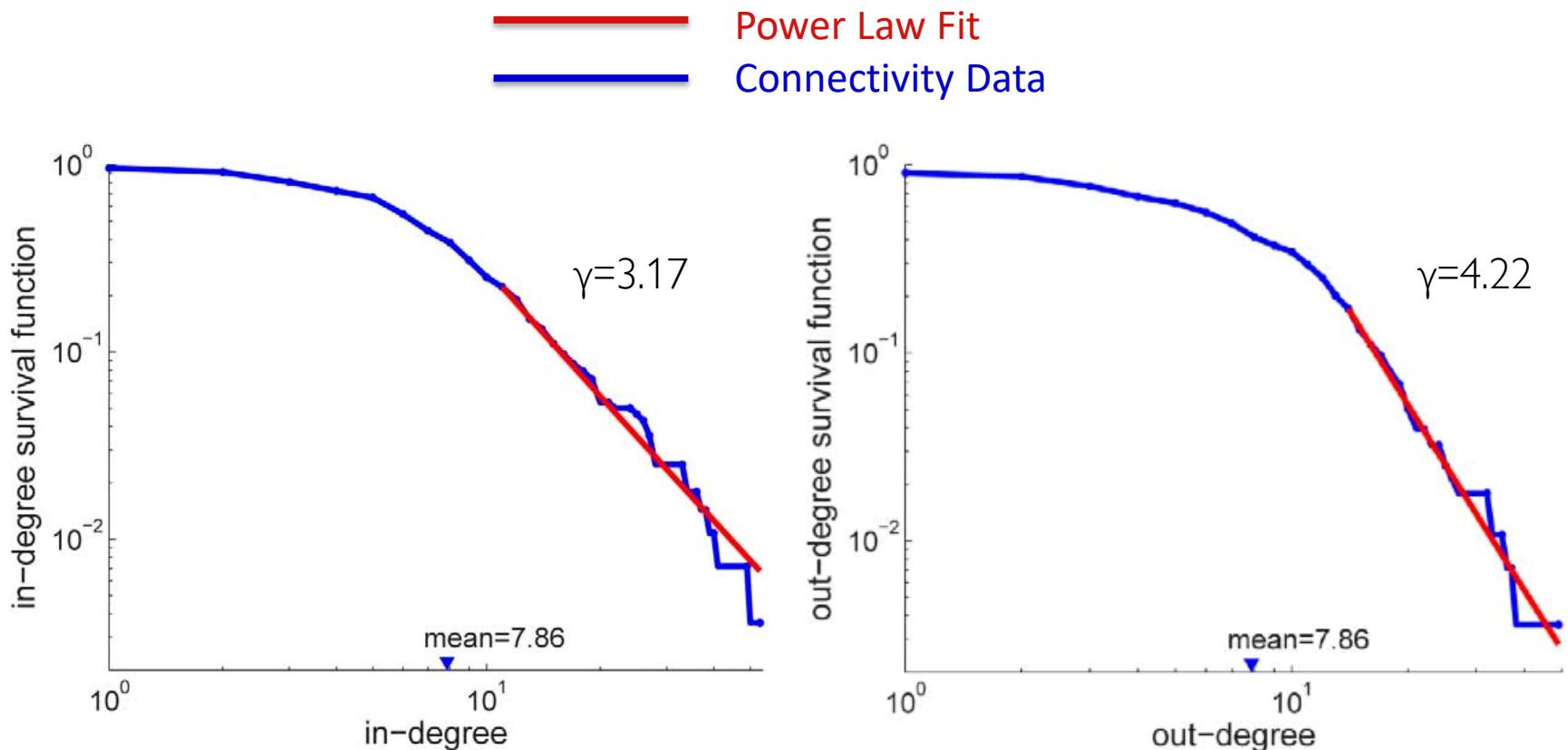
Real Networks: Low k behavior



- Power law is only good for asymptotic k
- Low k show binomial behavior



C. Elegans



Recap

- Graphs useful for two things from our perspective
 - Quantifying network connectivity
 - Formulating problems in easily-analyzable format
- Neural networks are
 - Clustered and connected
 - Have highly likely hubs
 - Best approximated by small-world priors: a mix of random and regular