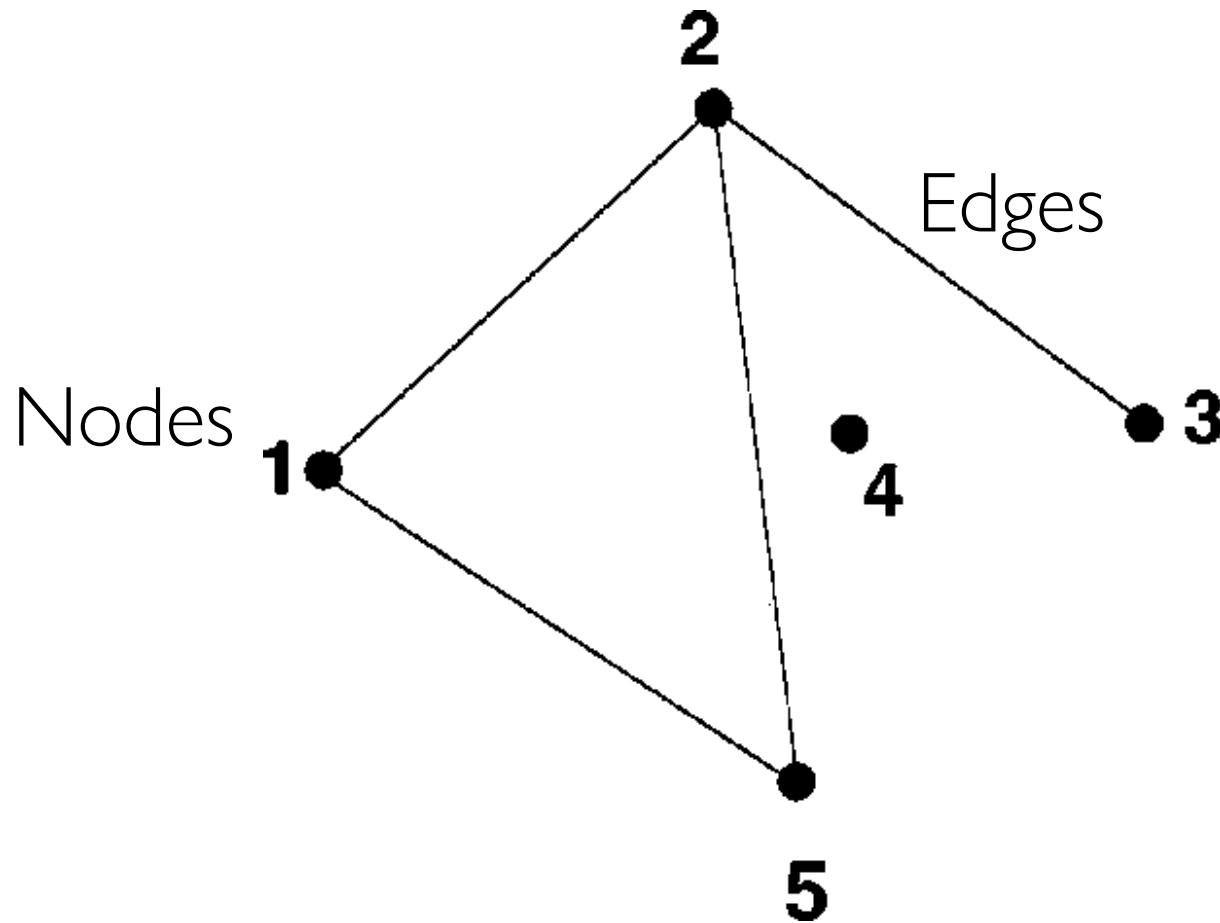


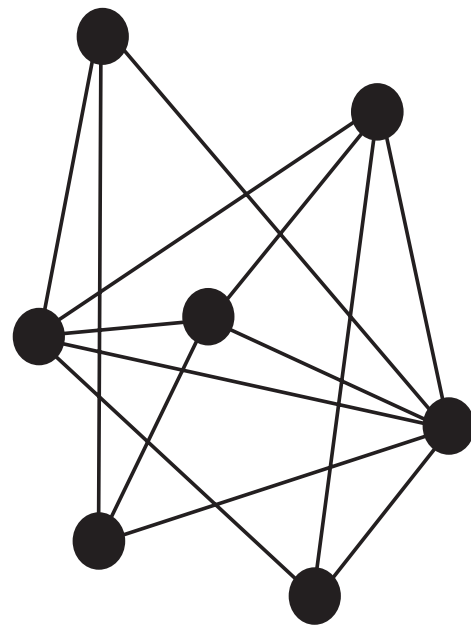
# Graph Theory and Connectivity

# What is a graph?

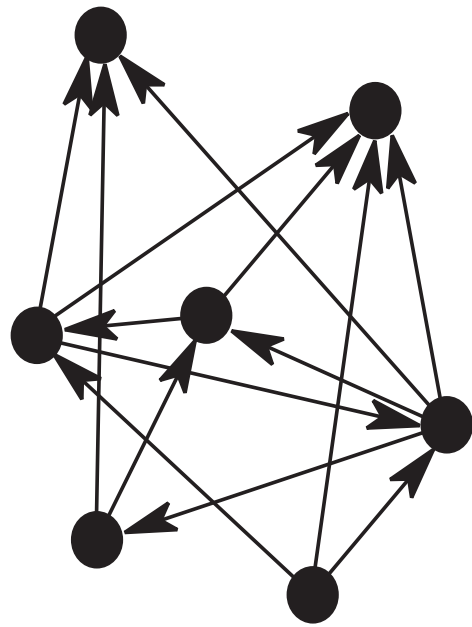




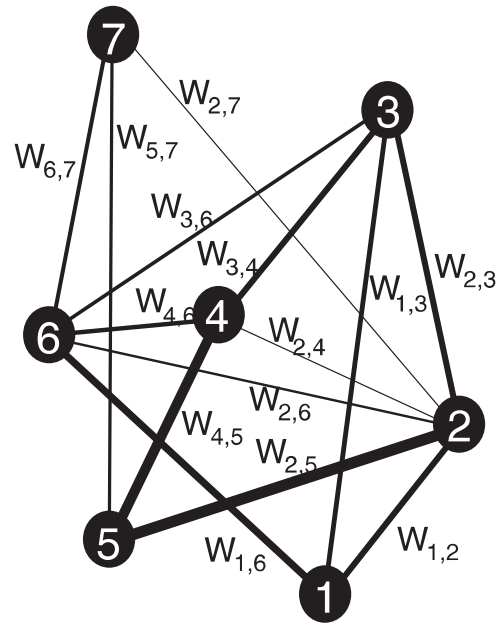
# Different types of graphs



Directed

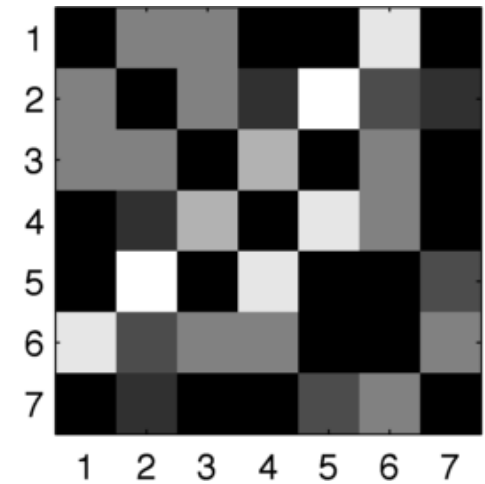
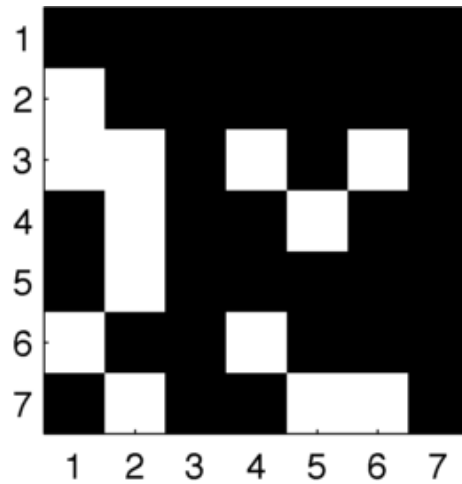
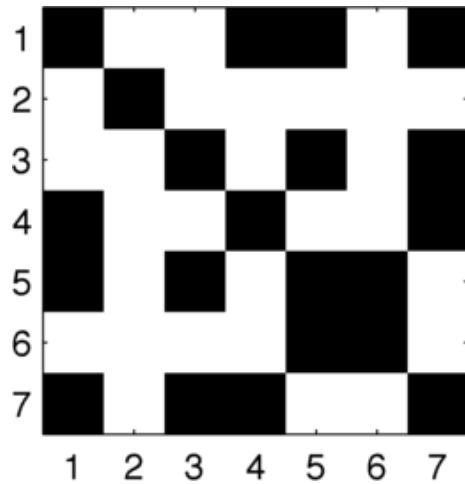
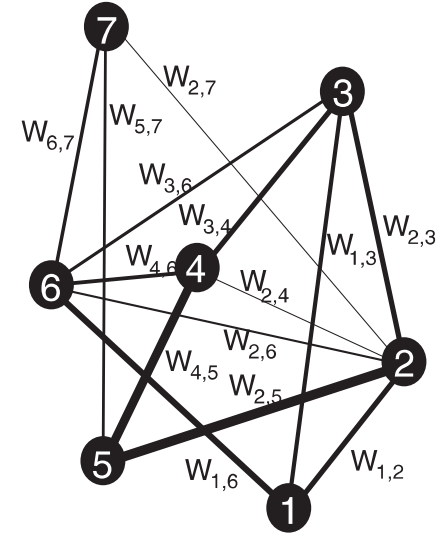
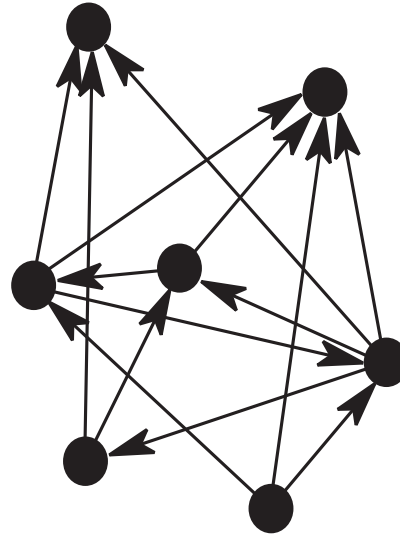
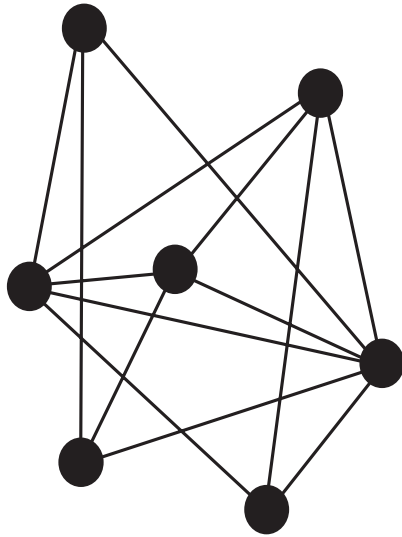


Weighted





# 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

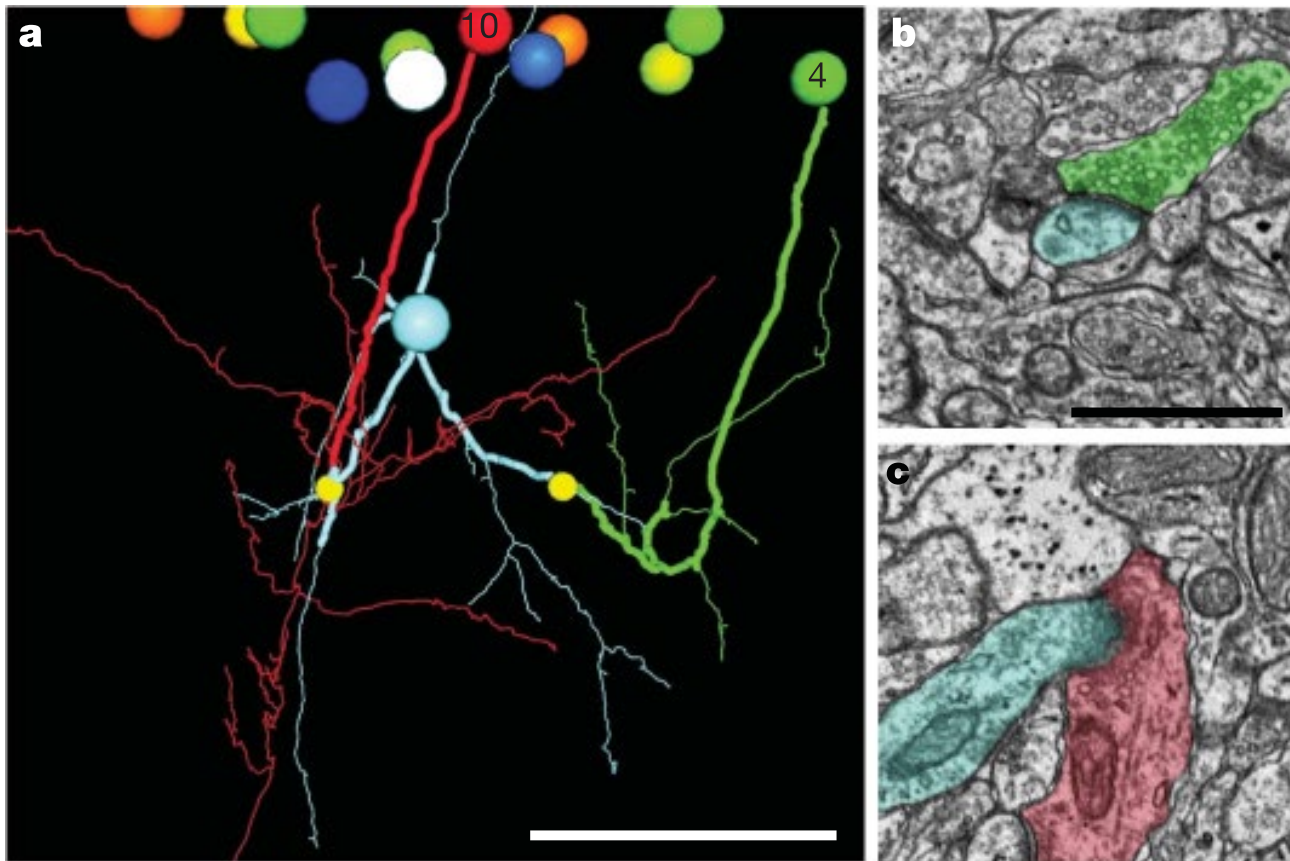


# Neurons are Connected

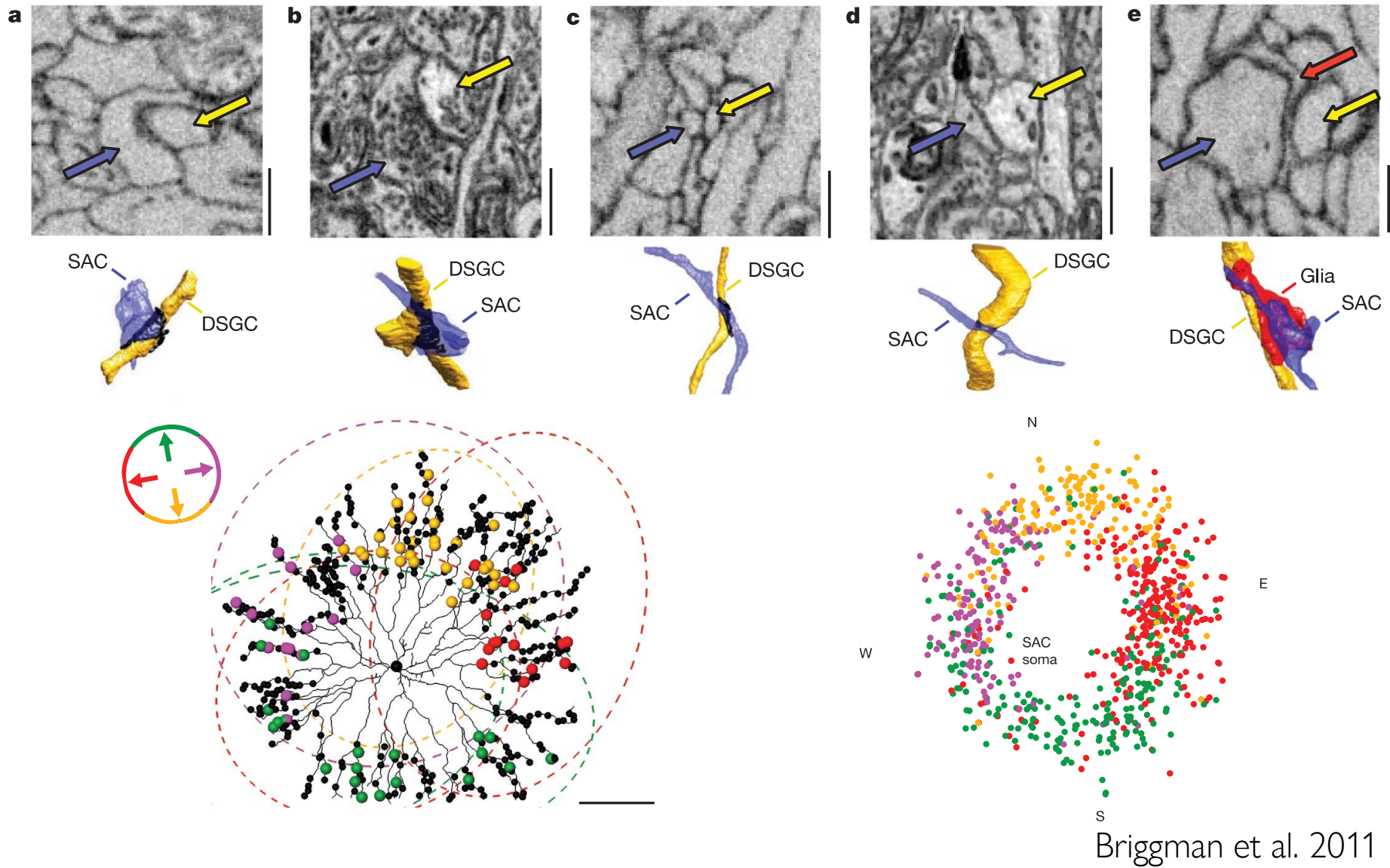
- How to measure neural connectivity?
  - Anatomical Connectivity
  - Effective Connectivity
  - Functional Connectivity



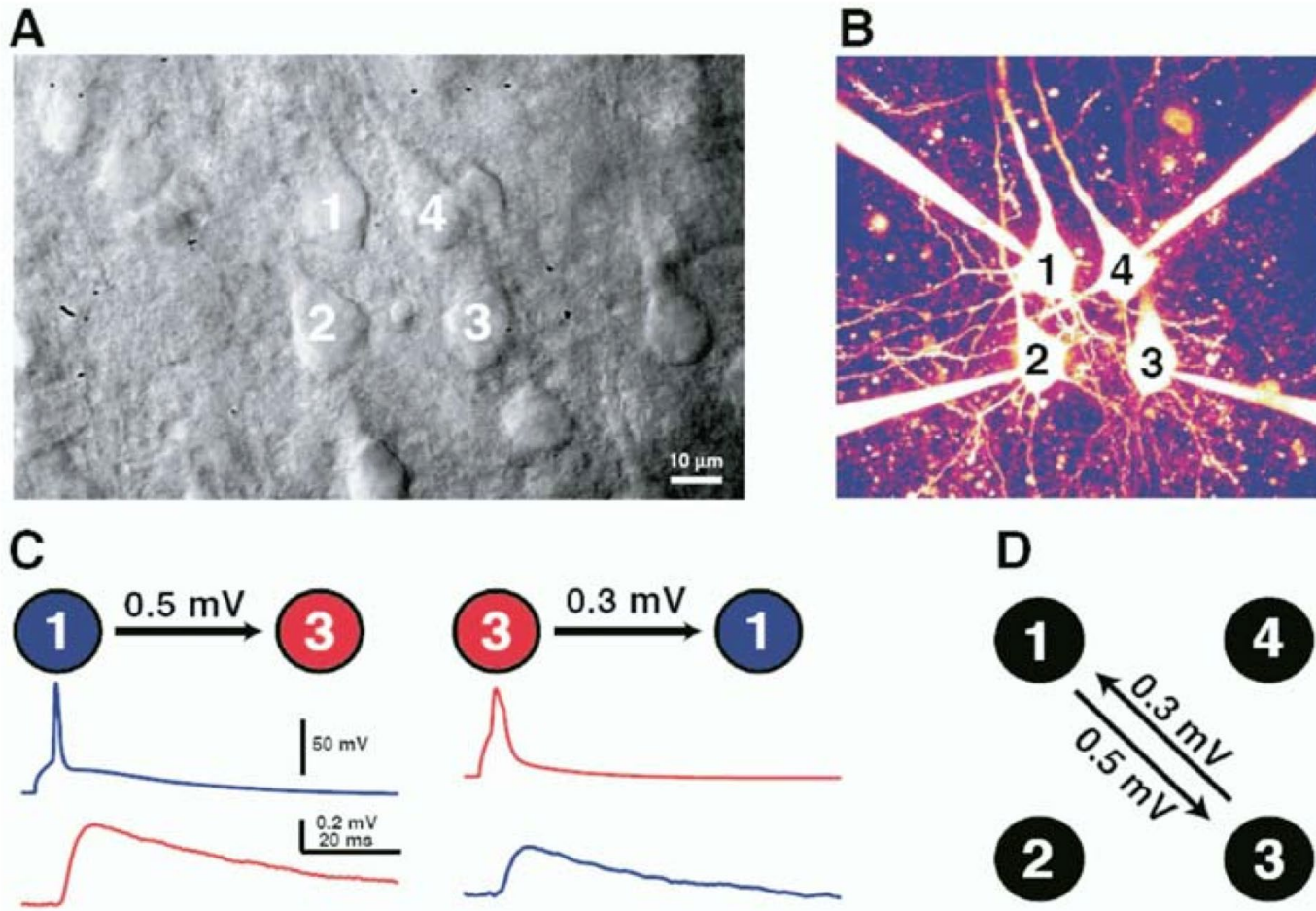
# Anatomical Connectivity



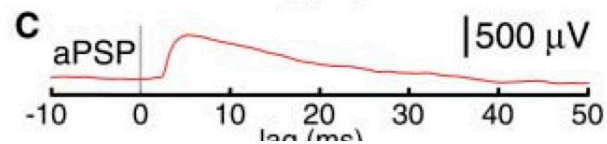
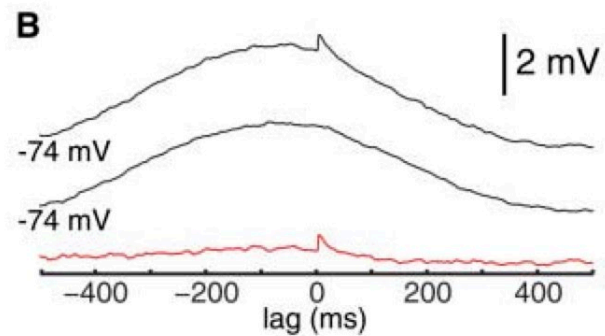
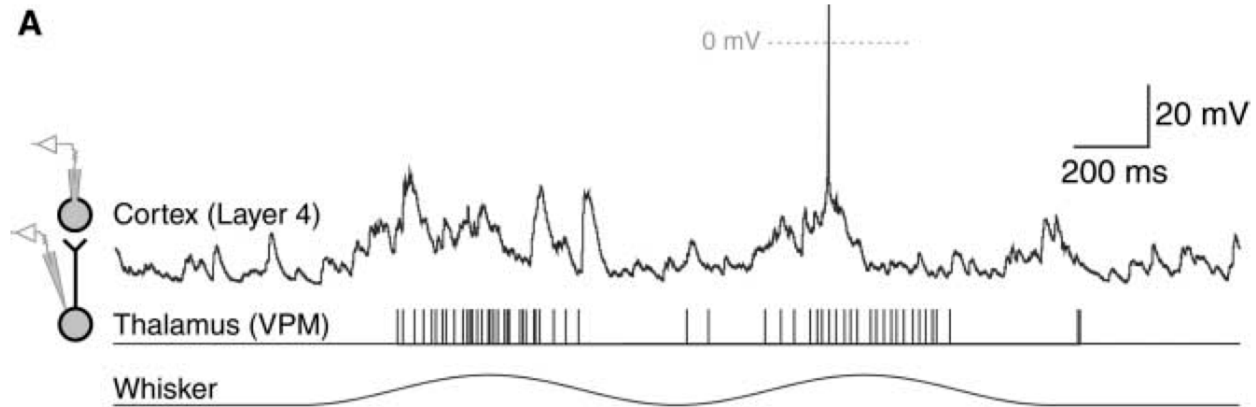
# Anatomical Connectivity



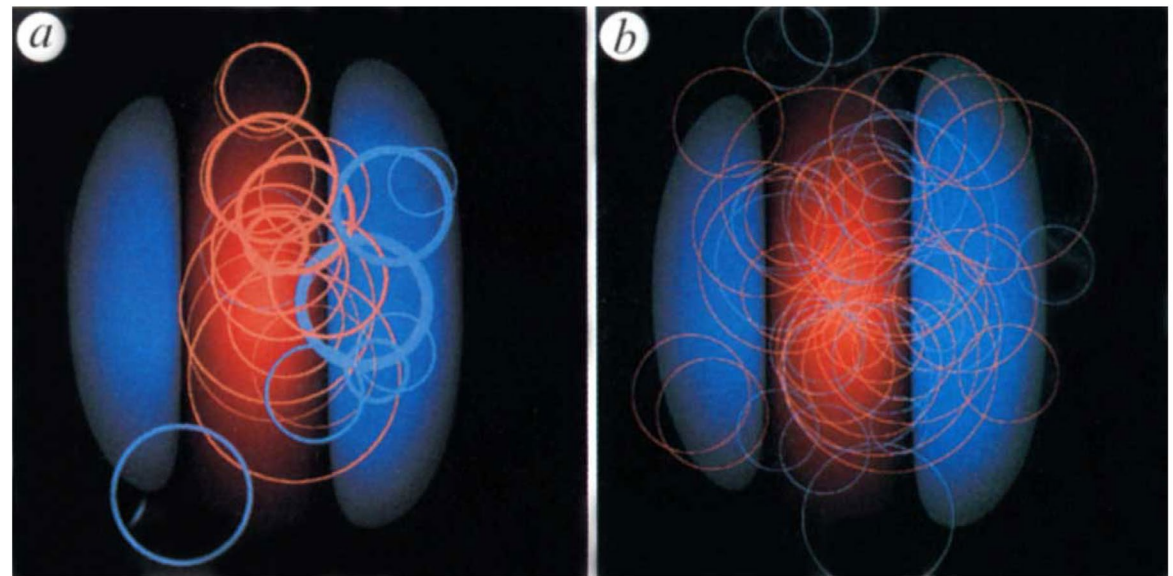
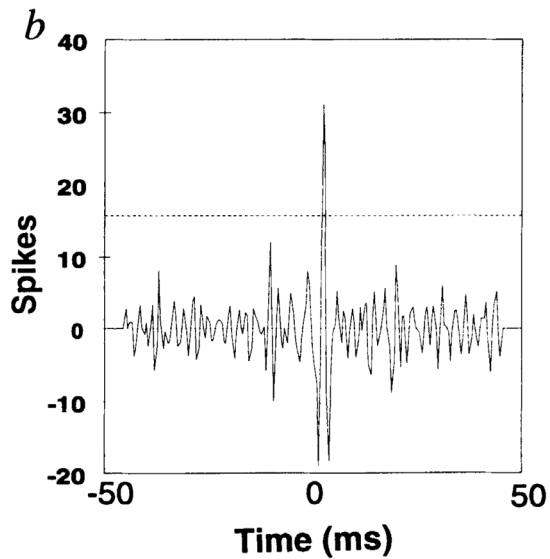
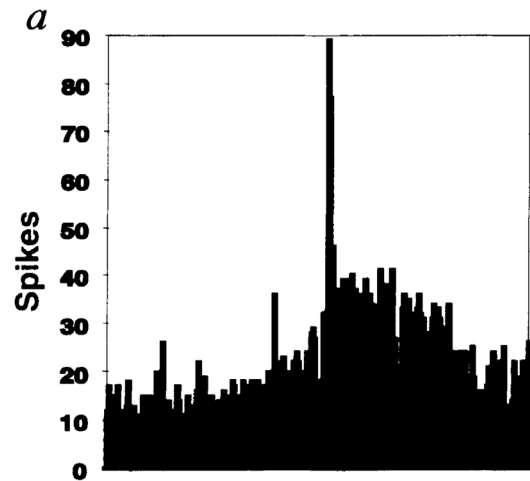
# Effective Connectivity



# Effective/Functional Connectivity



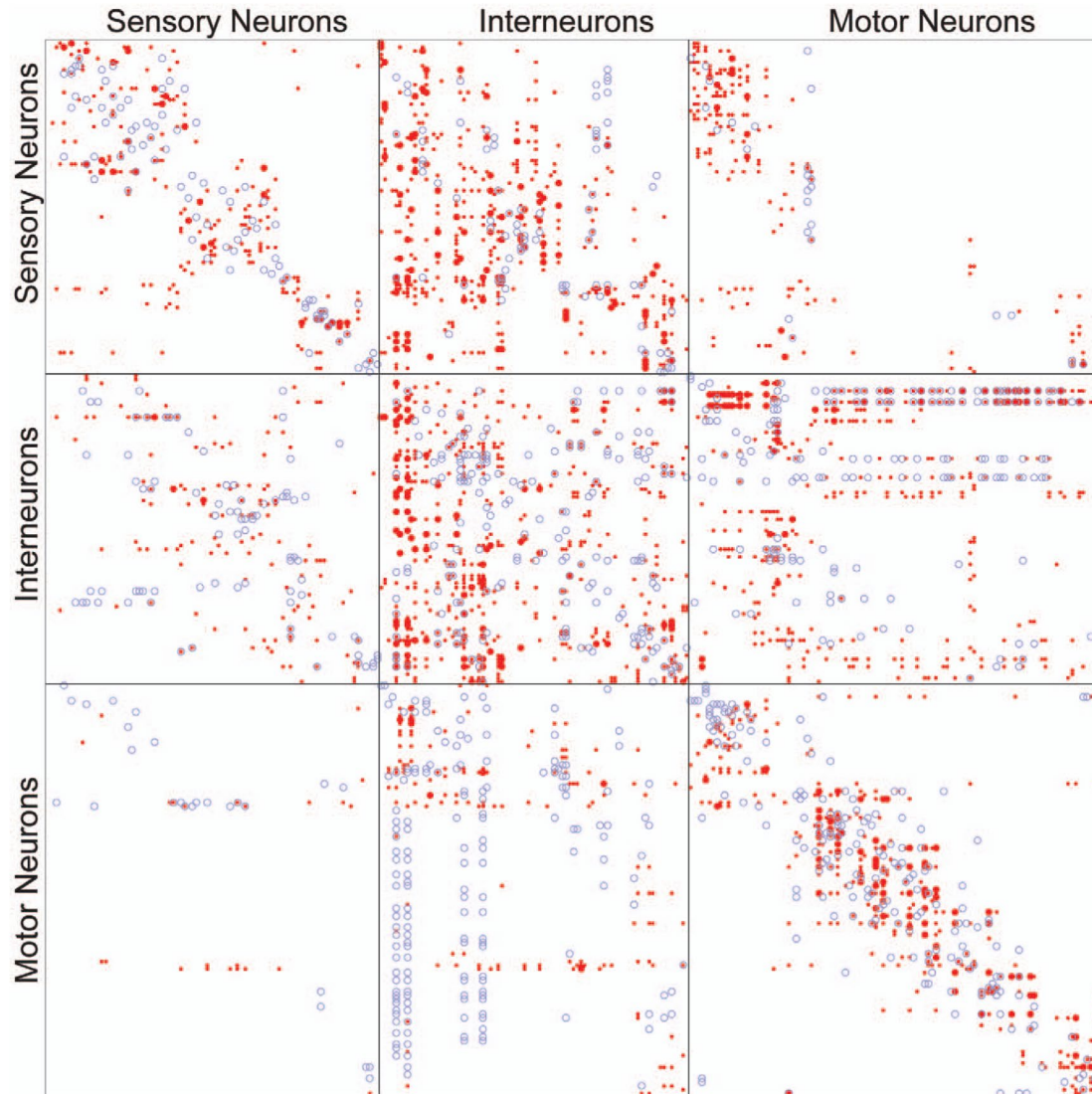
# Functional Connectivity



# 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

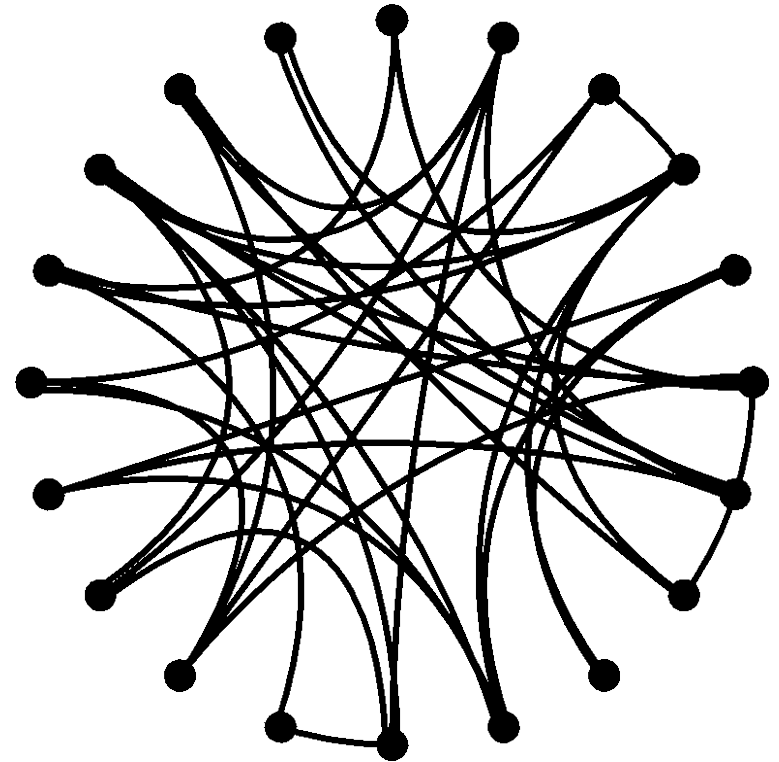


# Graph Priors

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

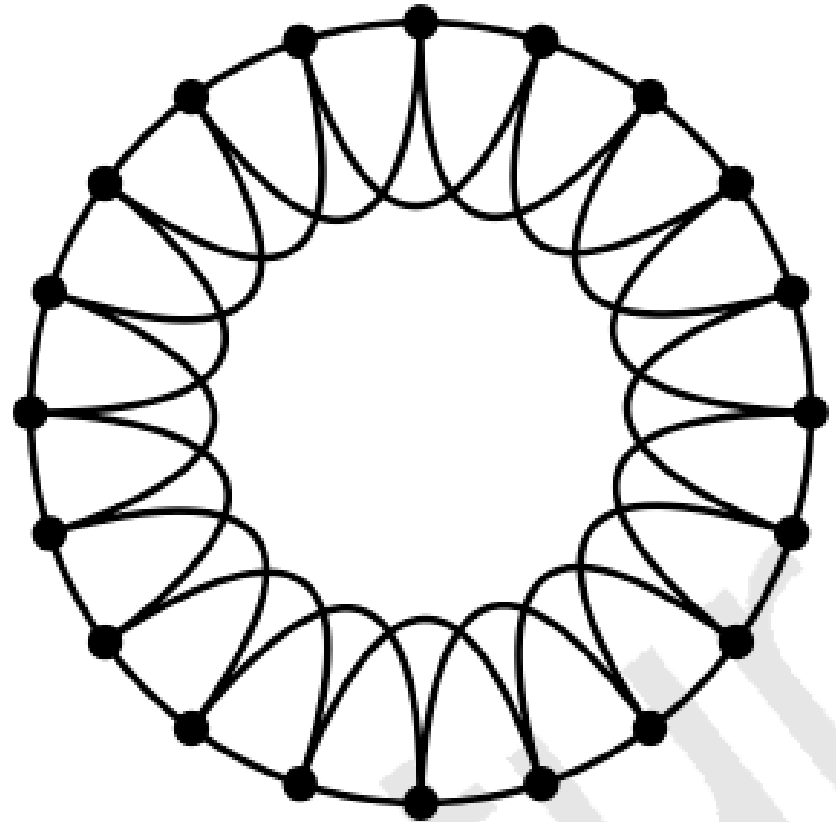
# Random Graphs

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



# Regular Graphs

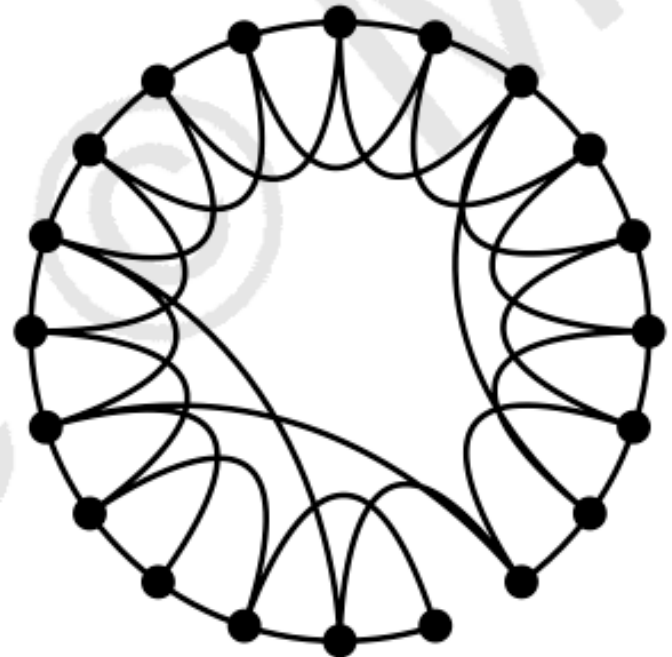
- Deterministic edge distributions
- Often determined by Euclidian distance



# Small-World Graphs

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

Small-world

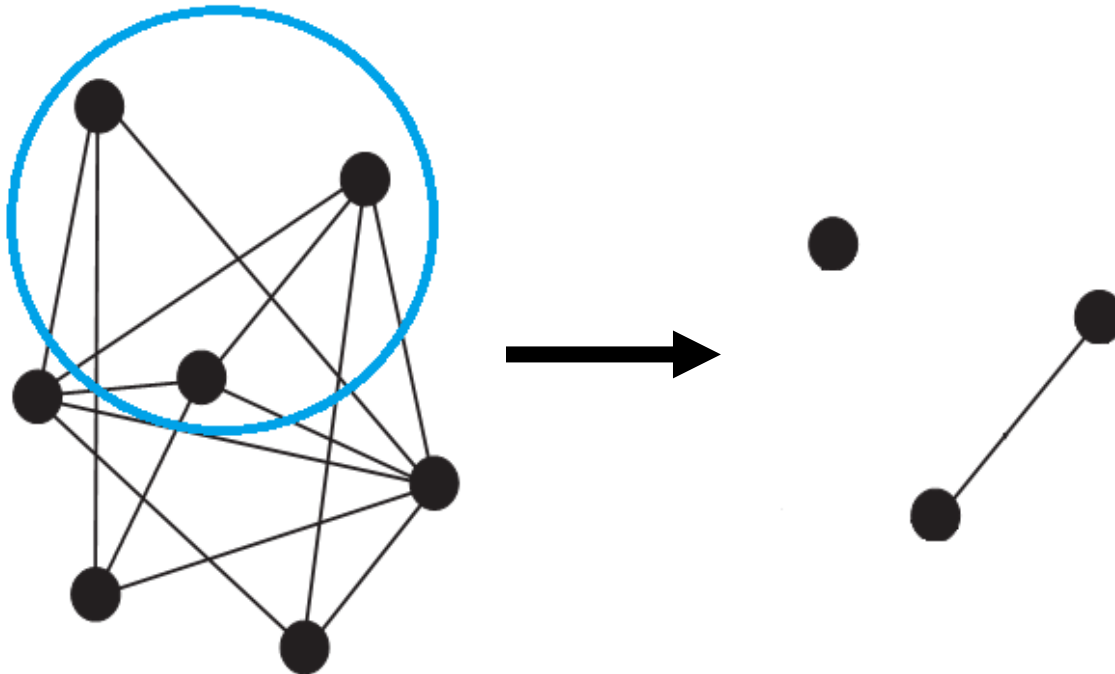


# Graph measures

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

# Motif Frequencies

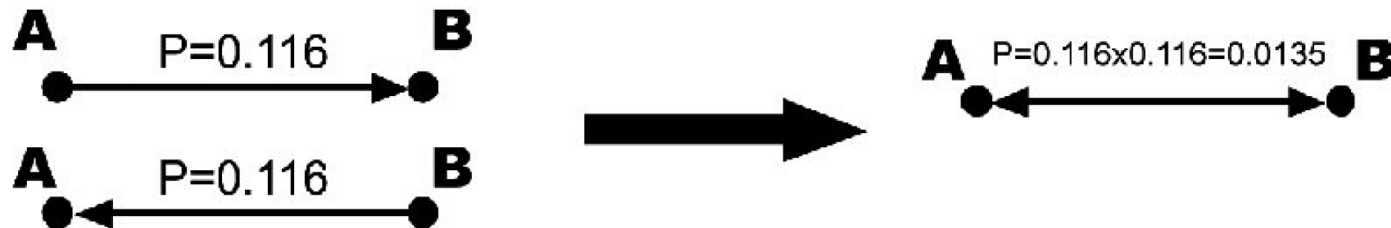
- *Subgraph*: A subset of nodes & their connected edges lifted from a larger graph



# Motif Frequencies

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

Null hypothesis assumes independent connection probabilities

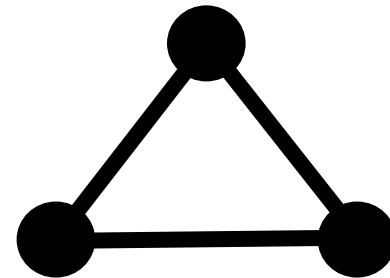


# Motifs: Random Prior

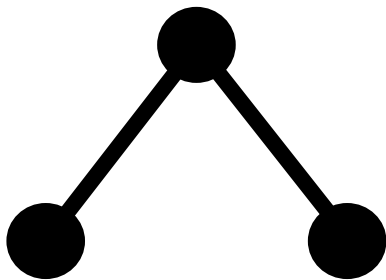
For simple, undirected, unweighted random graphs with connection probability  $p$ :



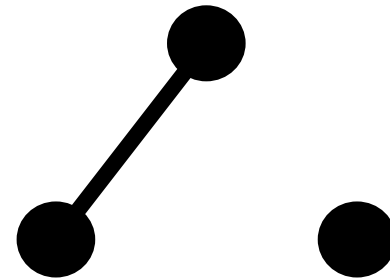
$$P(\text{edges}|\text{subgraph}) = p$$



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



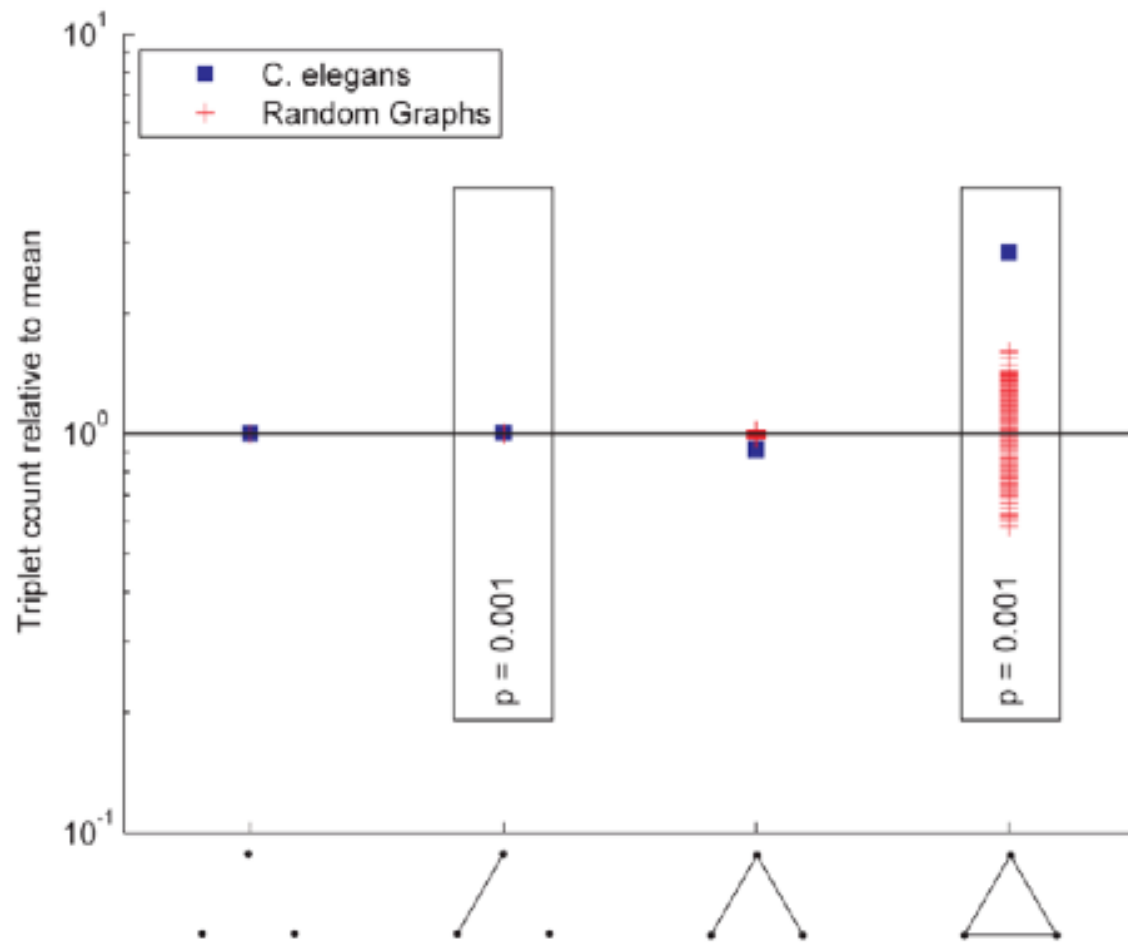
$$P(\text{edges}|\text{subgraph}) = C_2^3 p^2 (1 - p)$$



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



# Motifs: *C. elegans* vs. Random



# Clustering Coefficient

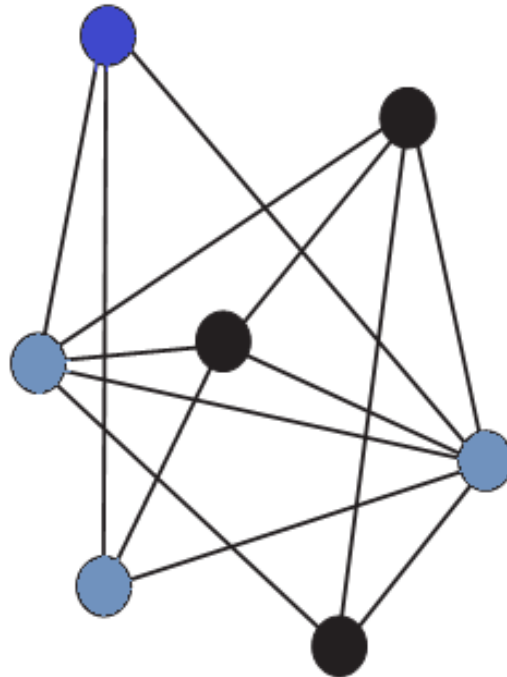
- *Complete Graph*: A graph of  $N$  nodes in which each node is connected to all other nodes in the network
- Complete subgraphs known as “cliques”
- For a simple, unweighted, undirected network:

$E \equiv$  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  $c_{jk}$ :

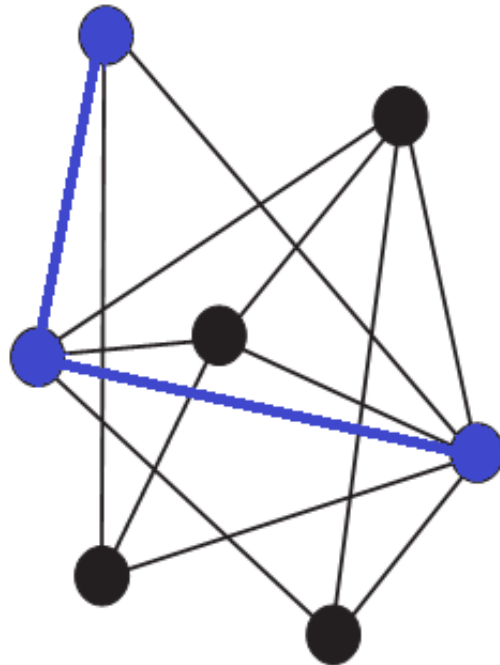
$$C_i = \frac{\sum_{j < k} c_{jk}}{\frac{1}{2} n_i (n_i - 1)}$$

- 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:

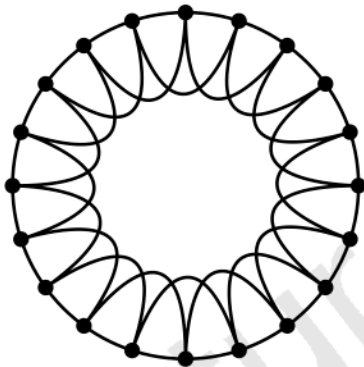
```
>> n = size(A,1);  
>> dists = [];  
>> for i = 1:n  
dtemp = Dijkstra(A,i);  
dtemp(i) = [];  
dists = vertcat(dists,dtemp);  
end  
>> mean(dists)
```



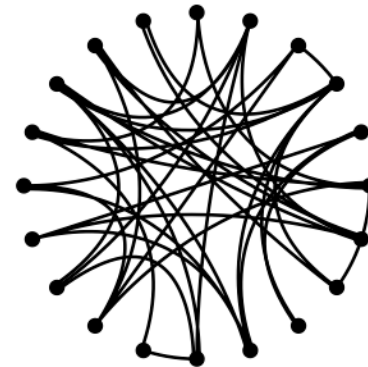
# L and C of prior graphs

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

Regular

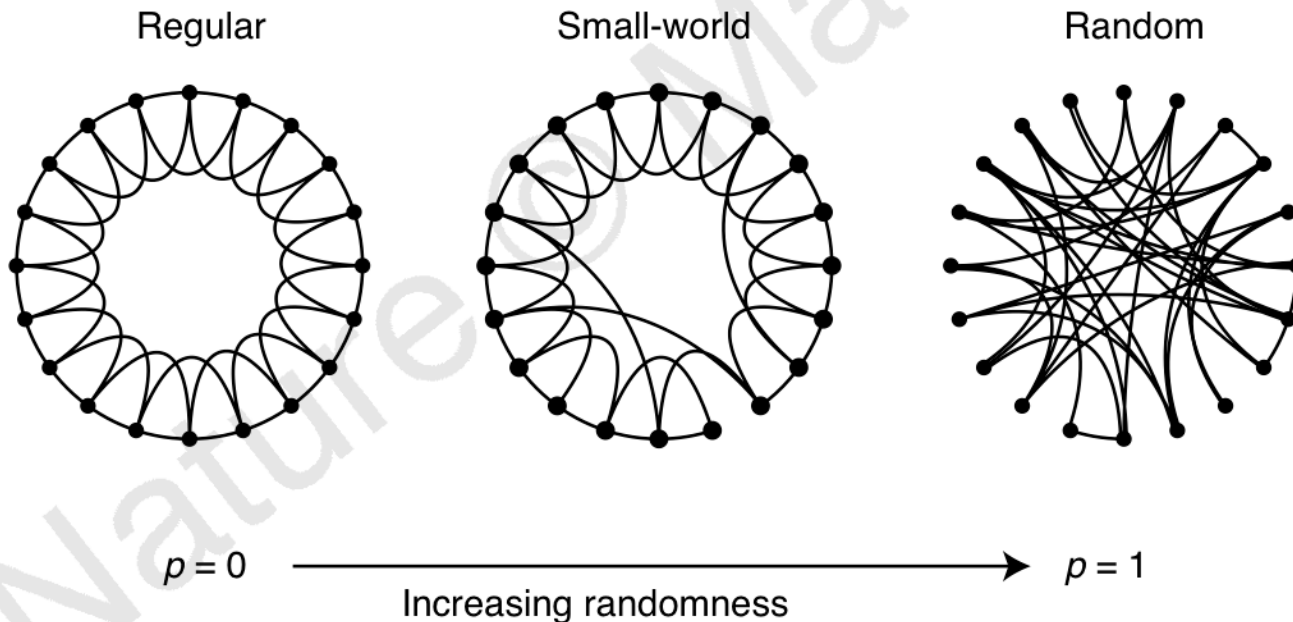


Random

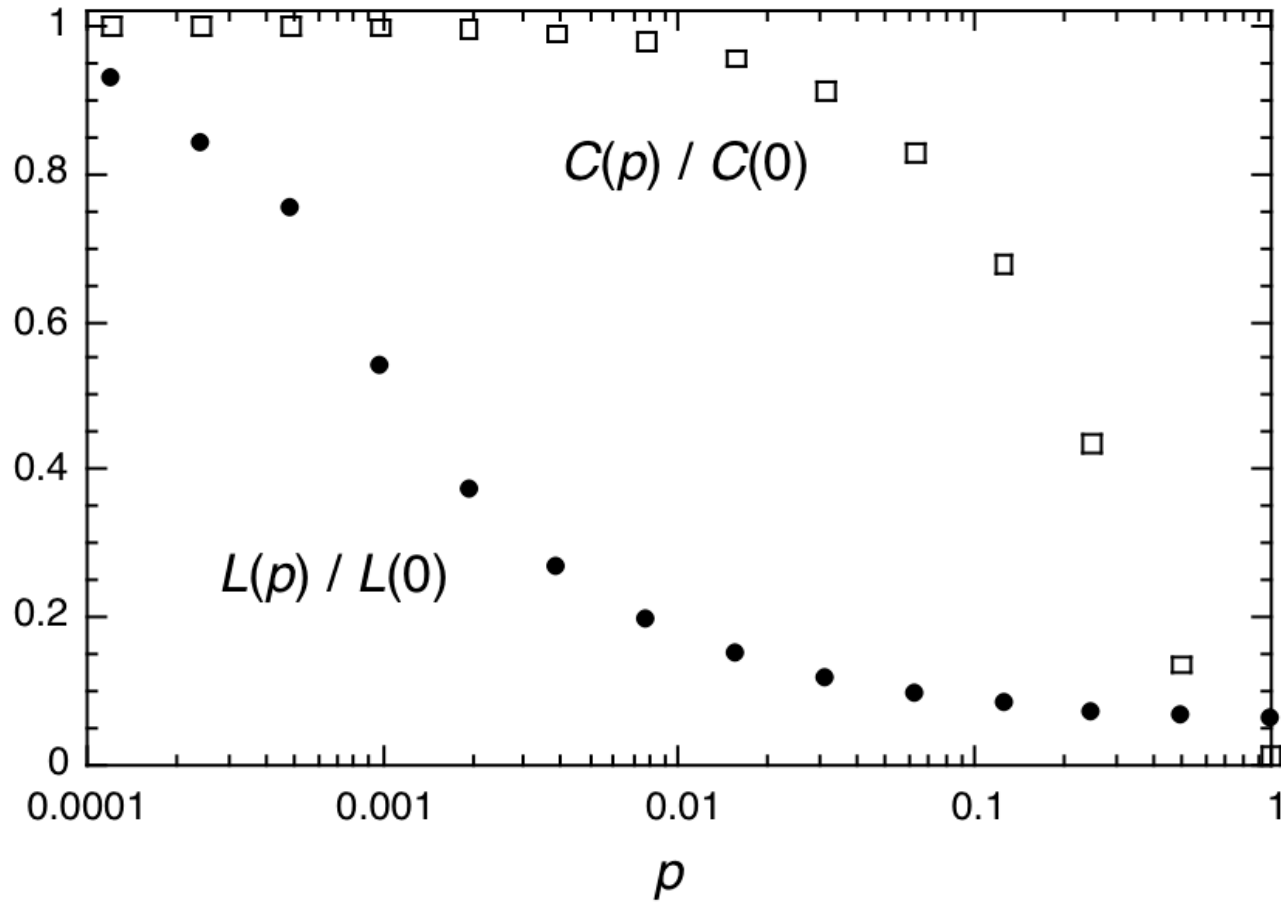


# L and C of prior graphs

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



# “Sweet Spot”



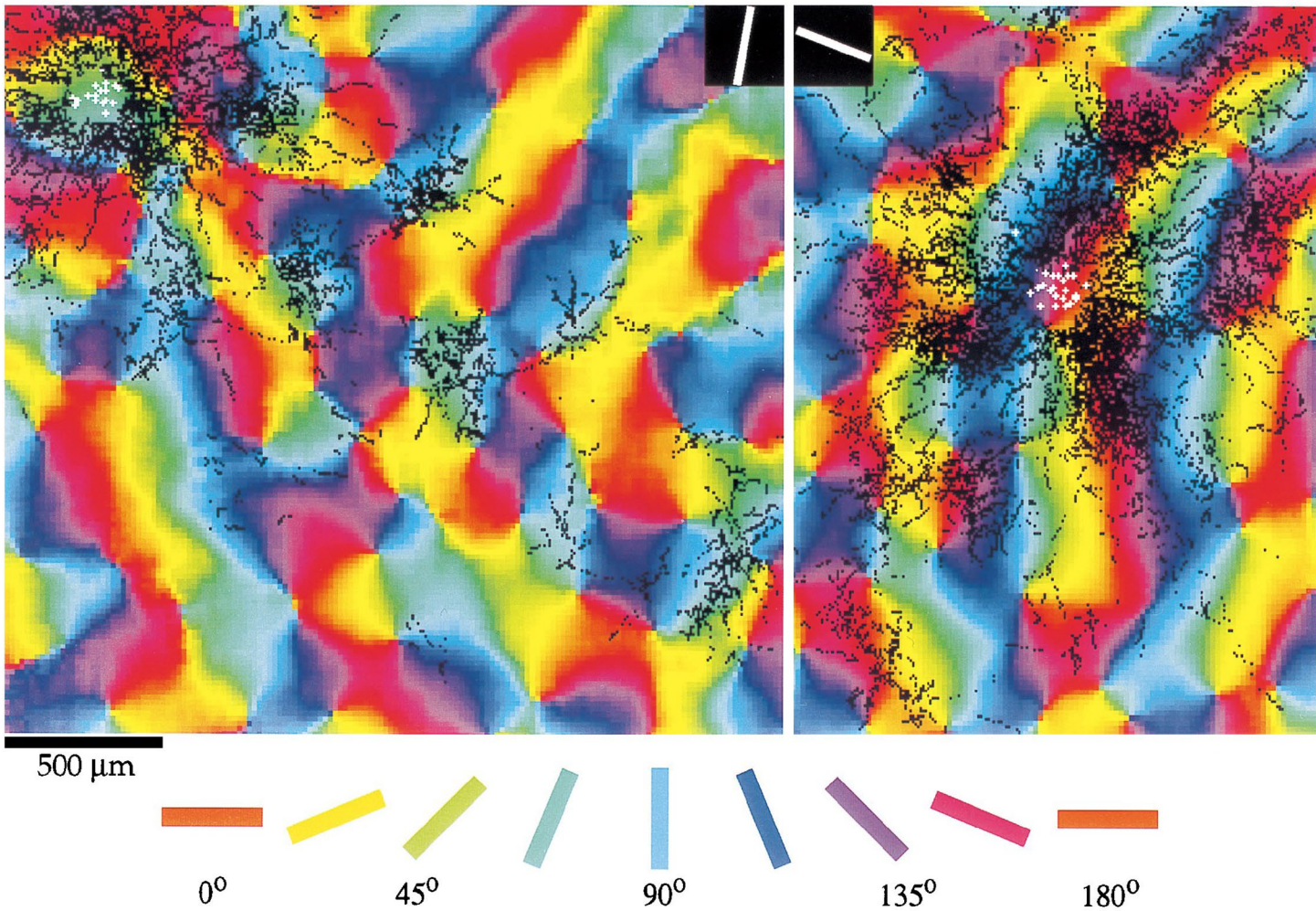
# Real Networks in the “Sweet Spot”

**Table 1 Empirical examples of small-world networks**

	$L_{\text{actual}}$	$L_{\text{random}}$	$C_{\text{actual}}$	$C_{\text{random}}$
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

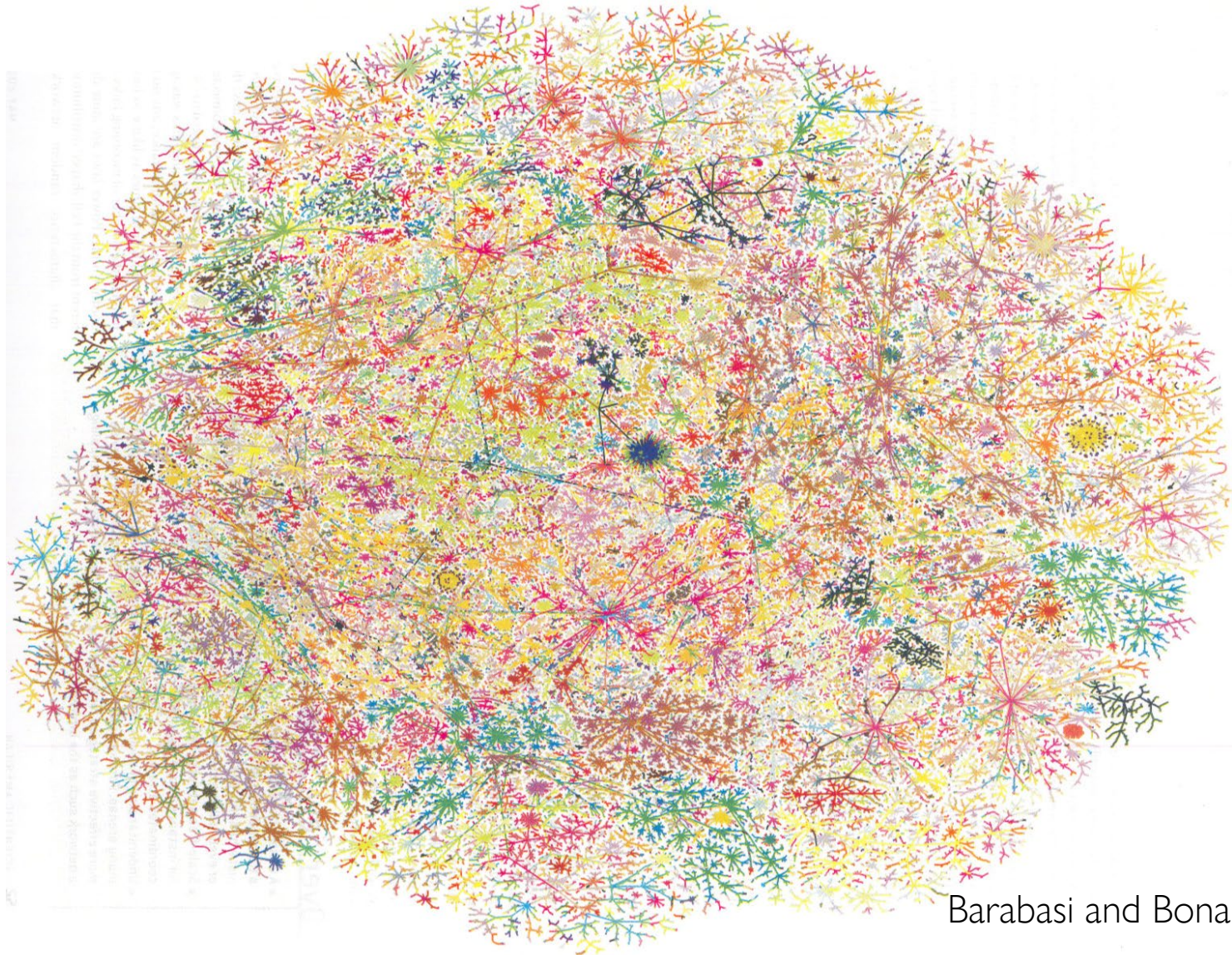
# Tree Shrew Small World



# 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

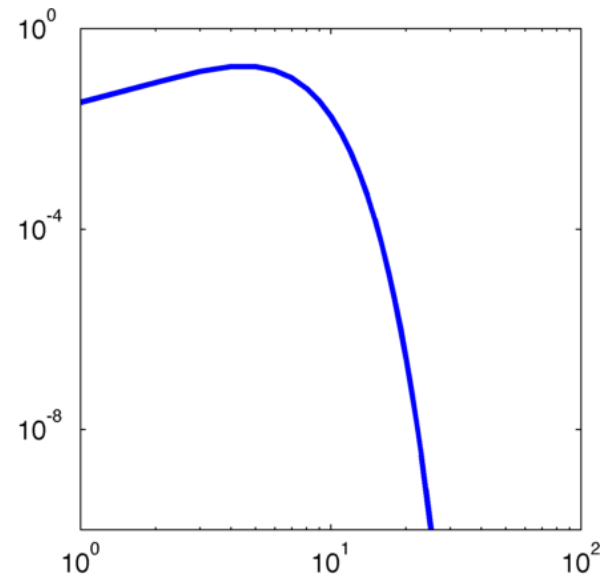
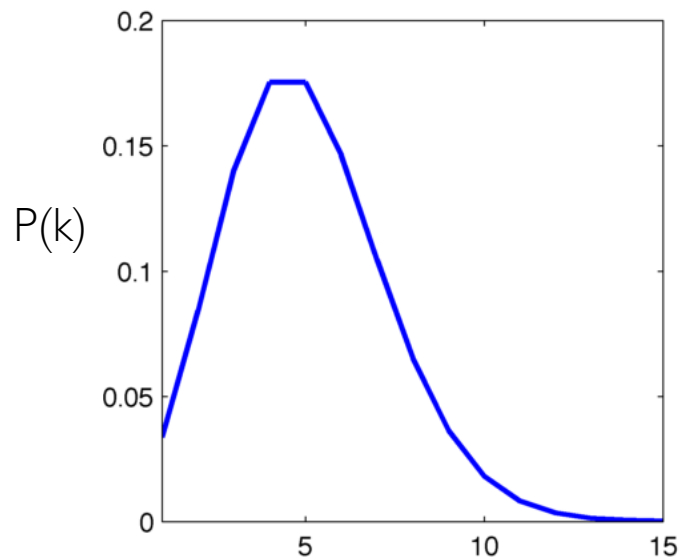


Barabasi and Bonabeau 2003

# Random Networks

- The degree distribution of a random network is:

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

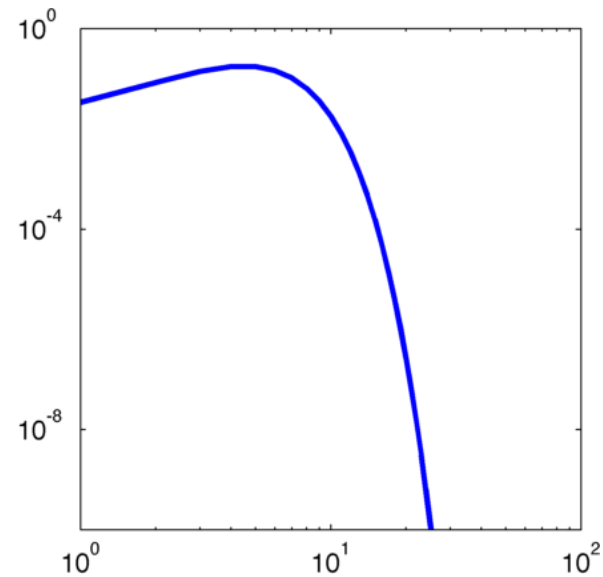
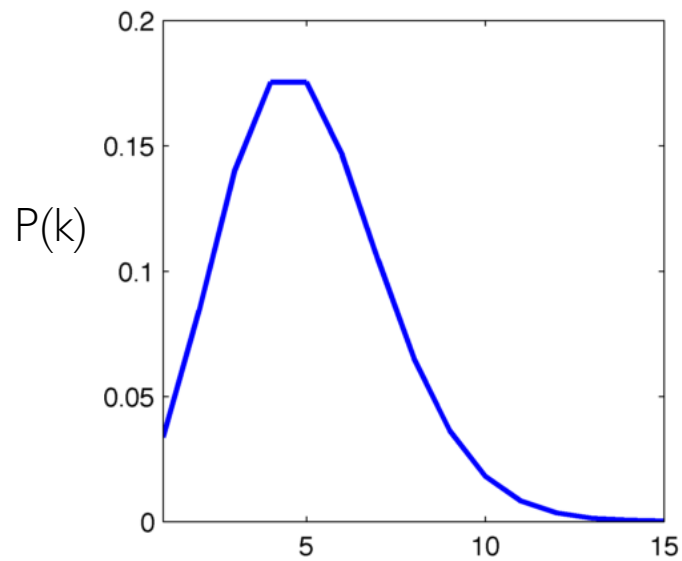




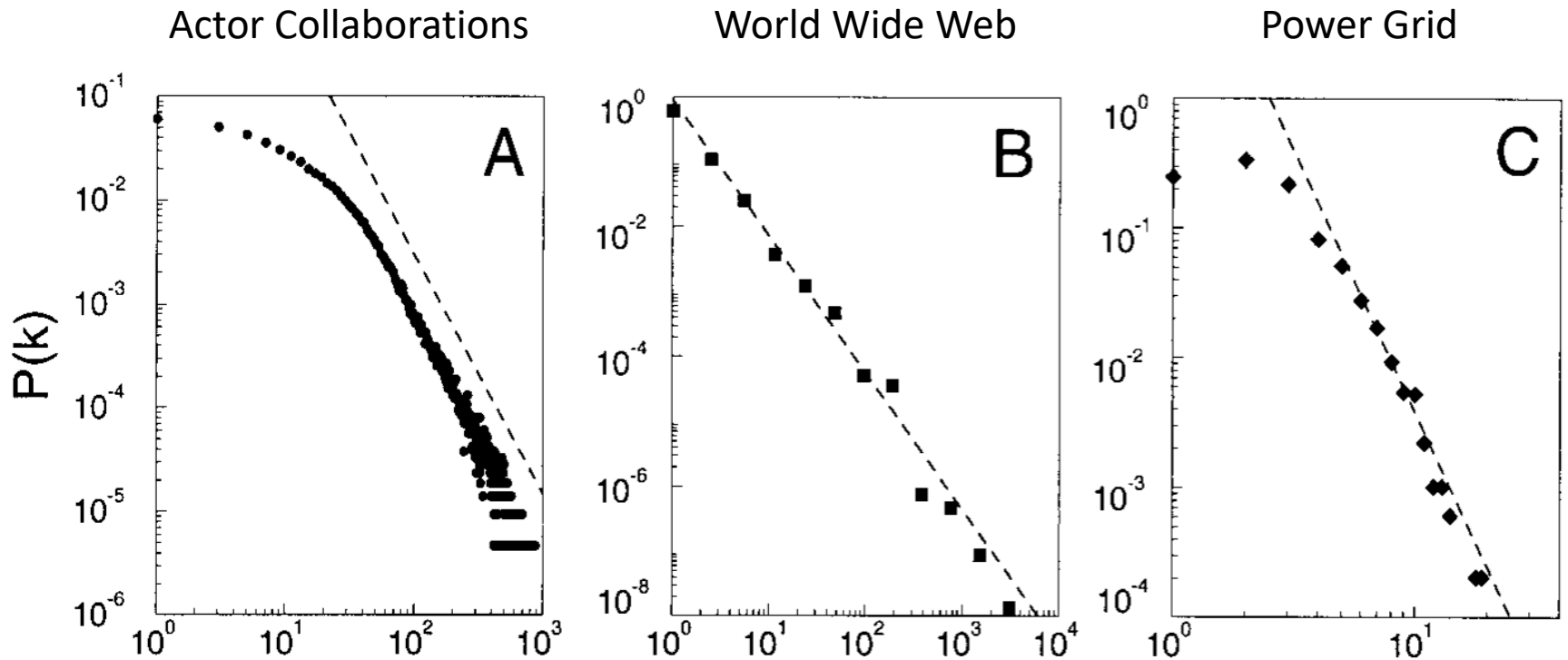
# Random Networks

- For random networks:

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



# Real Networks



- 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

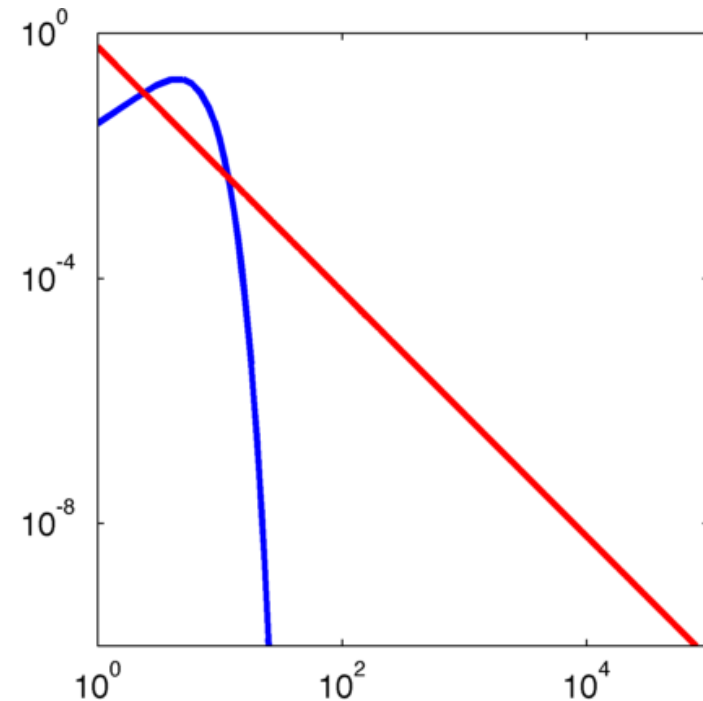
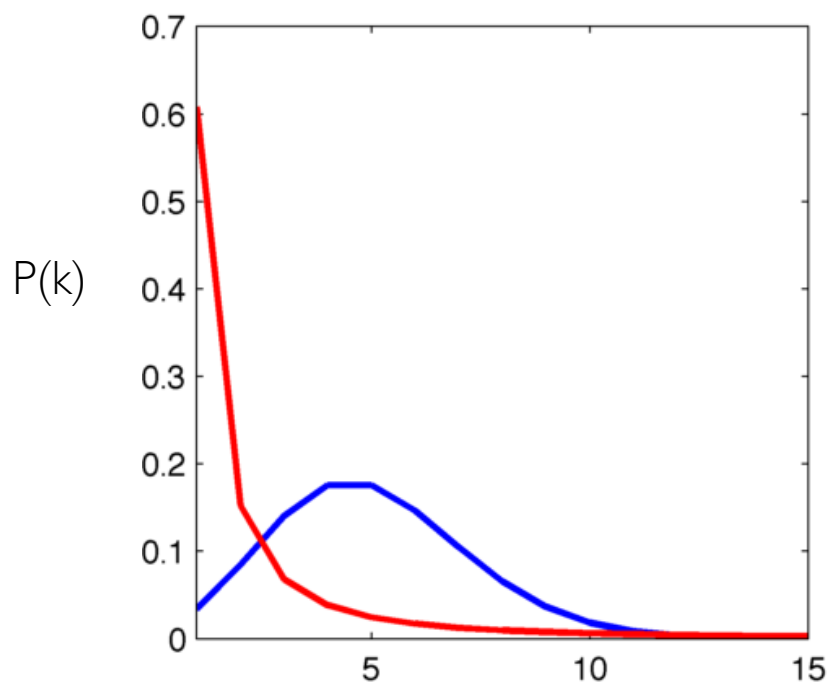
$$f(cx) = c^\gamma f(x)$$

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

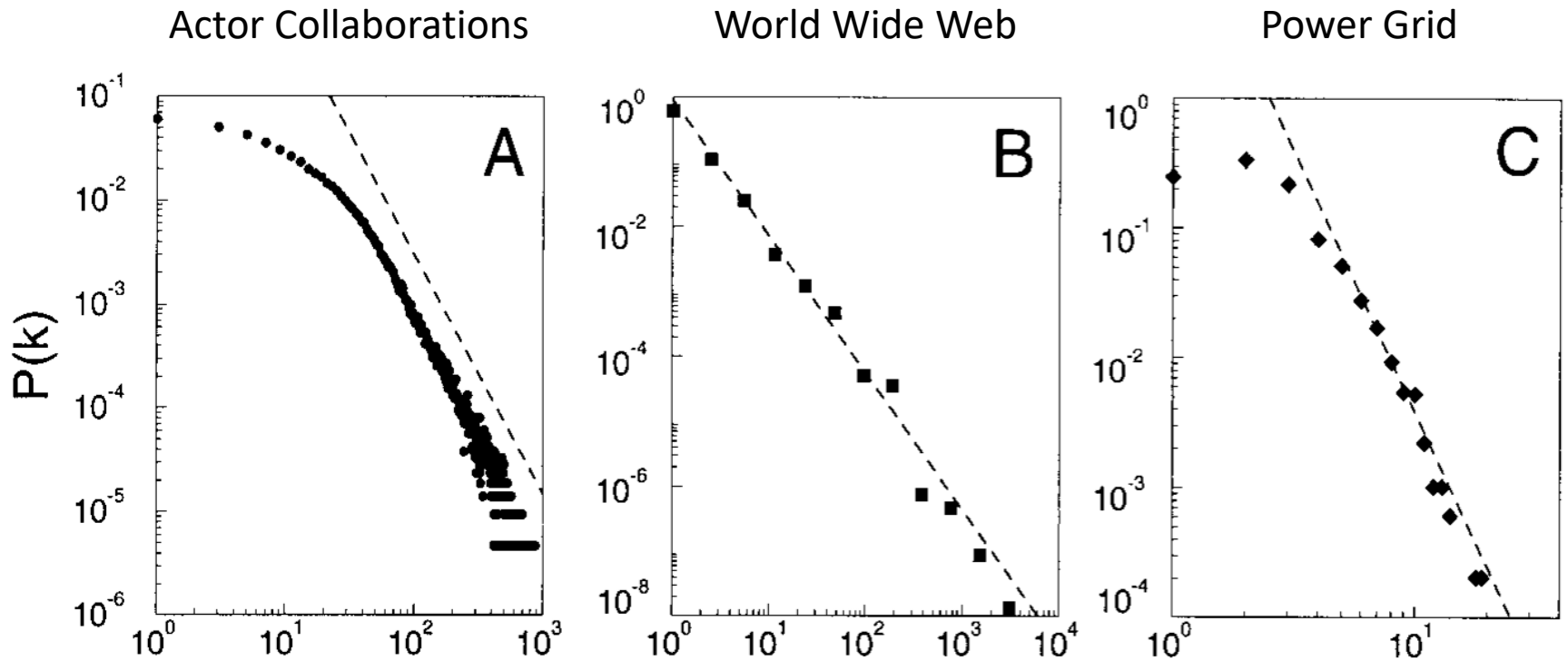
- Power laws lead to scale invariance
- A power law degree distribution defines a *'scale free' network*

# Scale Free Networks

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



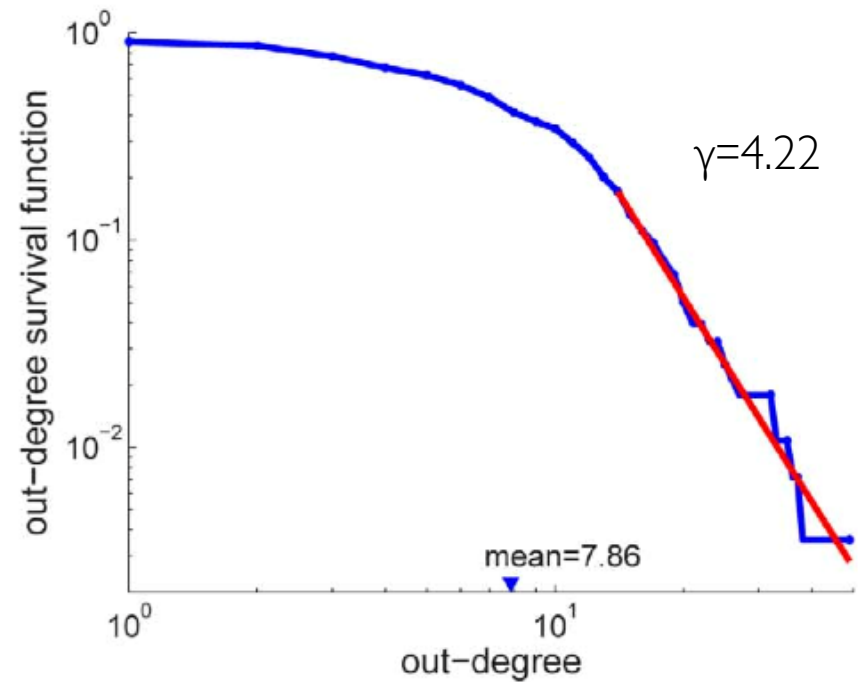
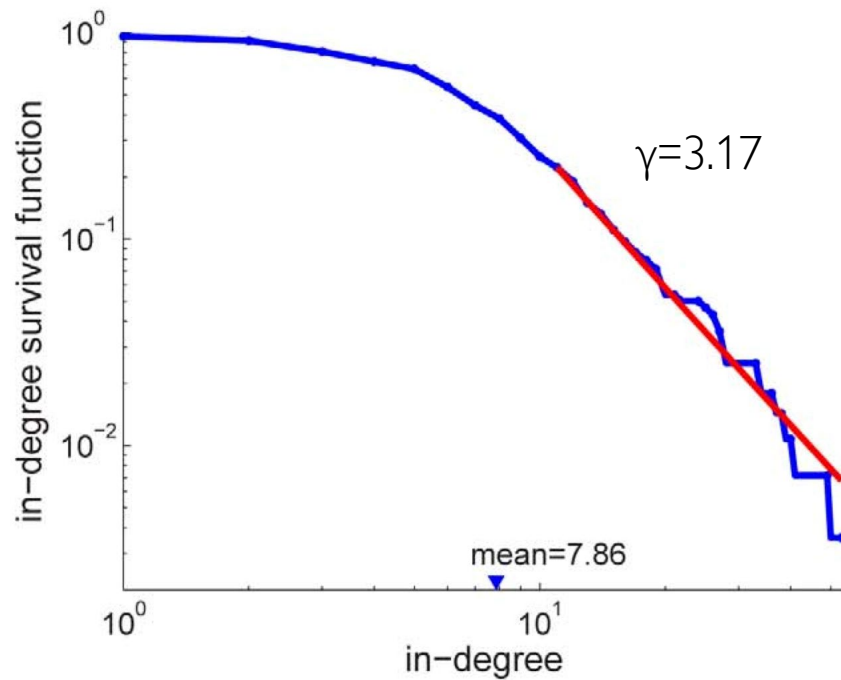
# Real Networks: *Low $k$ behavior*



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

# *C. Elegans*

— Power Law Fit  
— Connectivity Data



# 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