Imperial College London

Computational Neurodynamics

Topic 9
Dynamical Complexity

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Overview

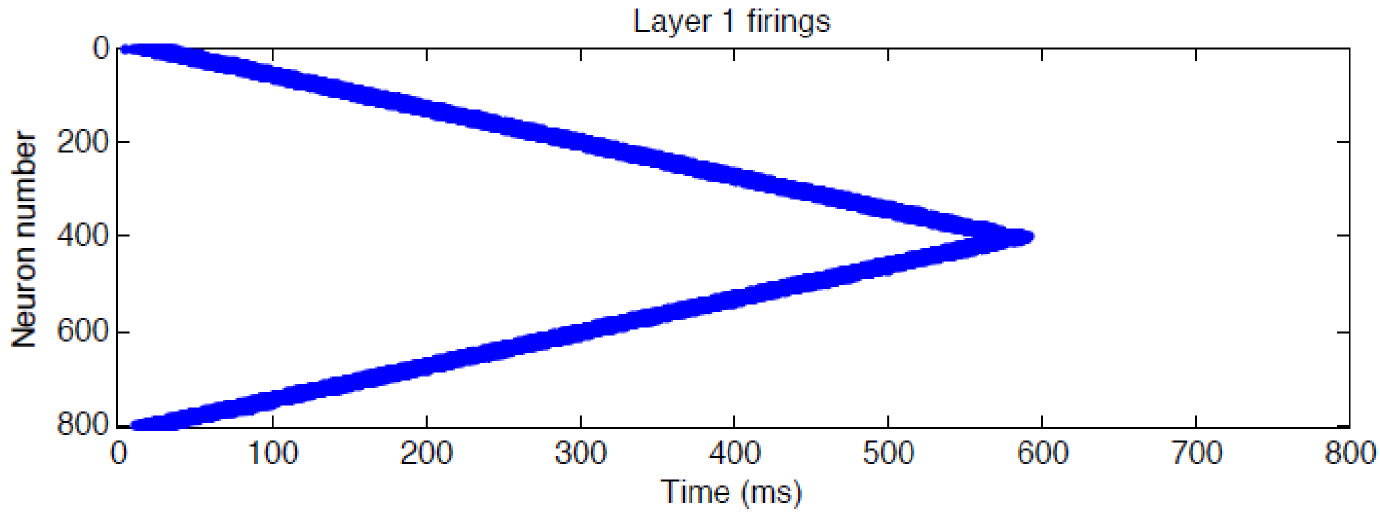
- Generating complexity
  - Watts-Strogatz neural networks
  - **Modular networks**
  - Spatially embedded networks
- Quantifying complexity
  - Dynamical Systems Theory
  - Information Theory

Complex Networks of Neurons

- Having looked at complex network topologies in the abstract, the next challenge is to understand complex networks of neurons
    - How does network topology influence dynamics?
    - Does a complex network give rise to complex dynamics?
    - What do we mean by dynamical complexity, and how can we measure it?
- Ultimately, we're interested in how the dynamics of the brain supports cognition, and indeed consciousness, in an embodied setting

Watts-Strogatz 1

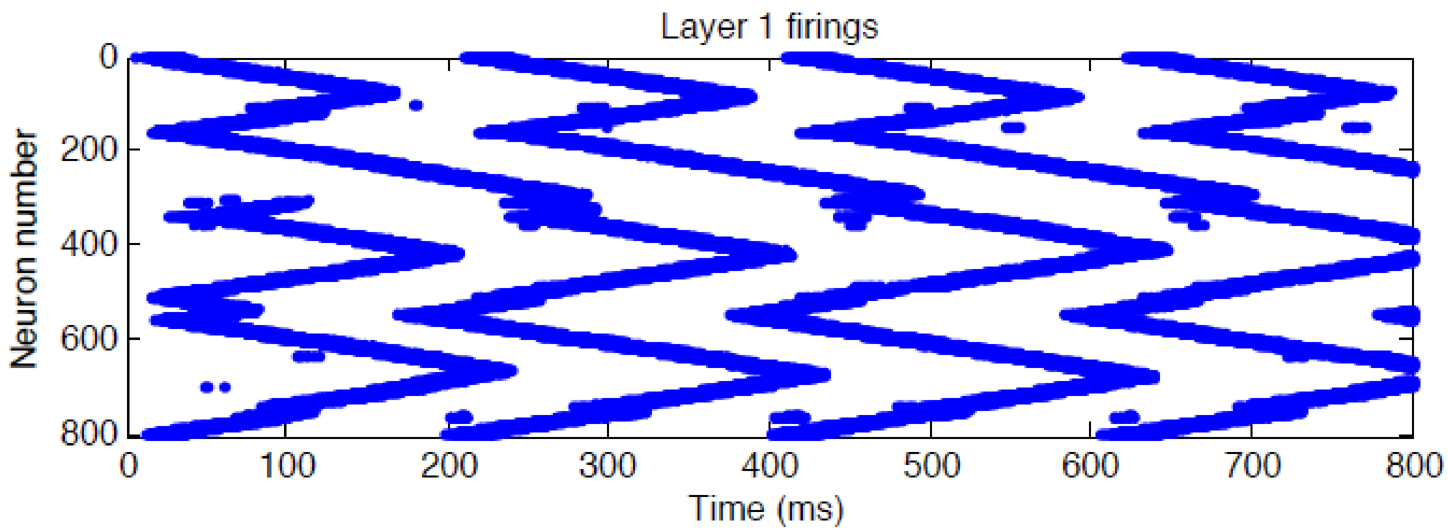
- First, let's consider Watts-Strogatz networks
- We will sweep the parameter p (rewiring probability) over a small range, using a network of 800 excitatory Izhikevich neurons. A single spike is injected at time 0 for neuron 1
- For p = 0, we get a wave of activation that eventually destroys itself



p = 0

Watts-Strogatz 2

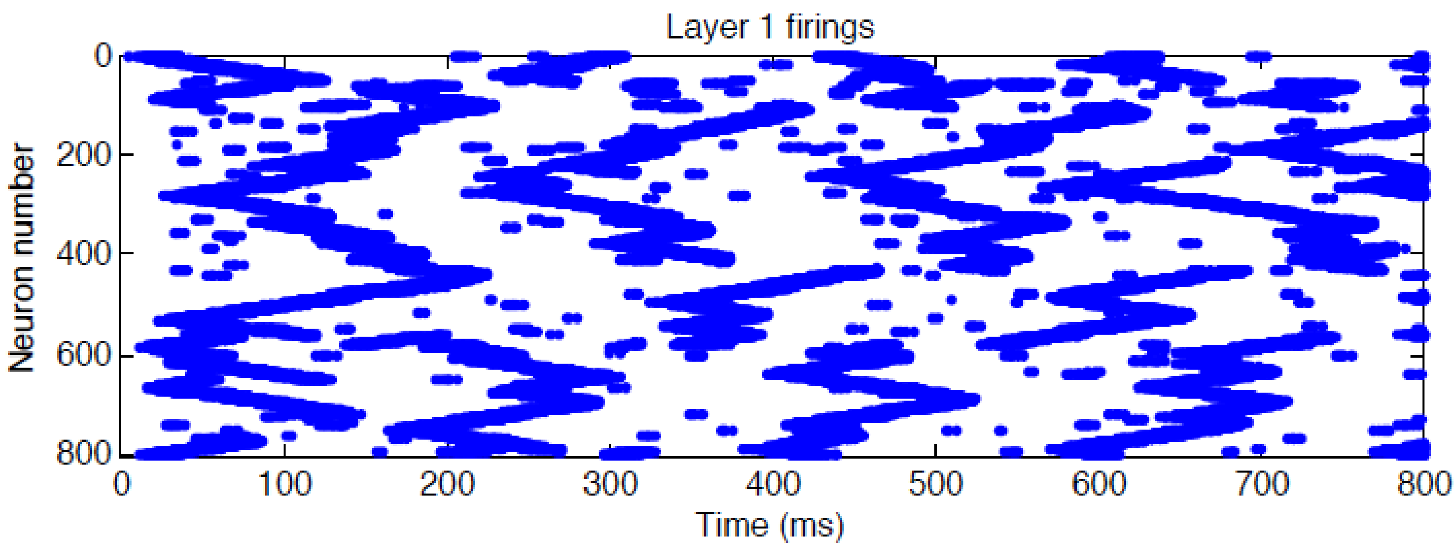
- When wavefronts meet, they annihilate each other
- If we let p = 0.01, then we obtain a small-world network
- The network then exhibits self-sustained activation. Thanks to the long-range connections, regions where activity has died out are re-ignited



p = 0.01

Watts-Strogatz 3

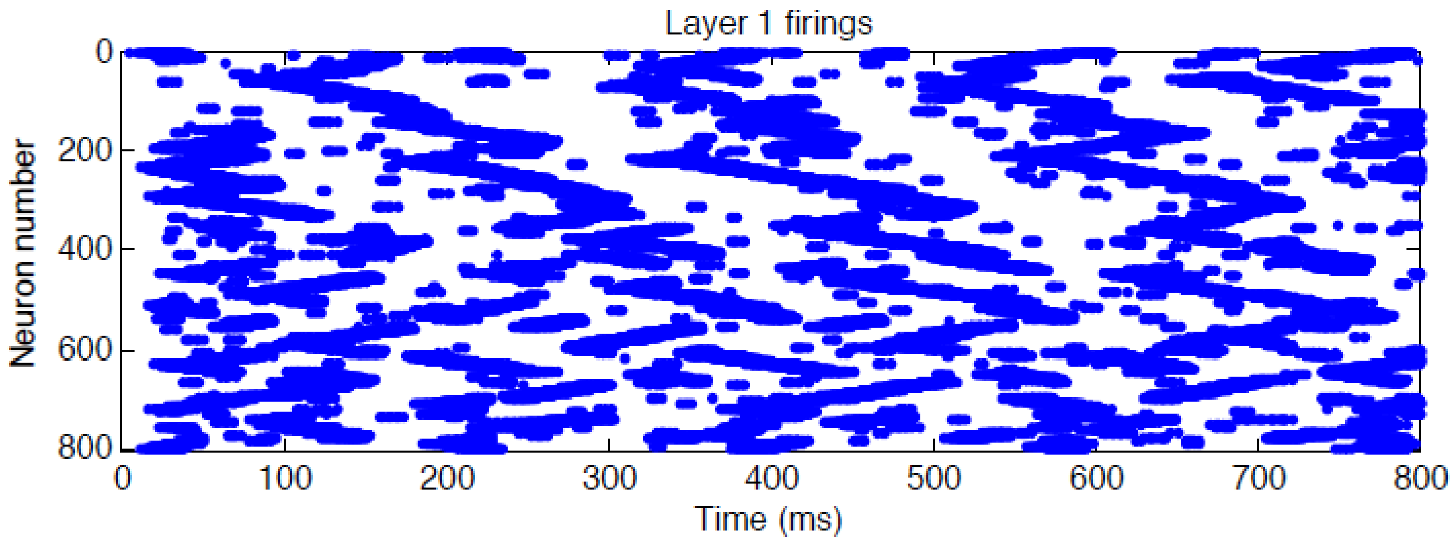
- With slightly higher p, we still get self-sustained activation. But there is no regular pattern
- Roxin & Riecke showed that in such a network there is chaotic activity with long transients



p = 0.05

Watts-Strogatz 4

- As p increases, the waves of activation tend to break up more
- This is all very interesting. But the Watts-Strogatz procedure doesn't produce networks that are biologically plausible. Real brain networks do not resemble a ring lattice



$p = 0.1$

Structure and Dynamics

- Although a network based on a ring-lattice is not a very good model of a real neural network, the exercise of sweeping values of p has revealed something important, which is that *network structure dramatically influences dynamics*
- Each of the Watts-Strogatz networks we have looked at has exactly the same number (and statistically the same types) of neurons, and the same number of connections
- Their only difference is the network topology, the organisation of connections
- To study this further, let's look at *modular* networks constructed using the rewiring method, and sweep a range of values for the rewiring probability p in a similar way

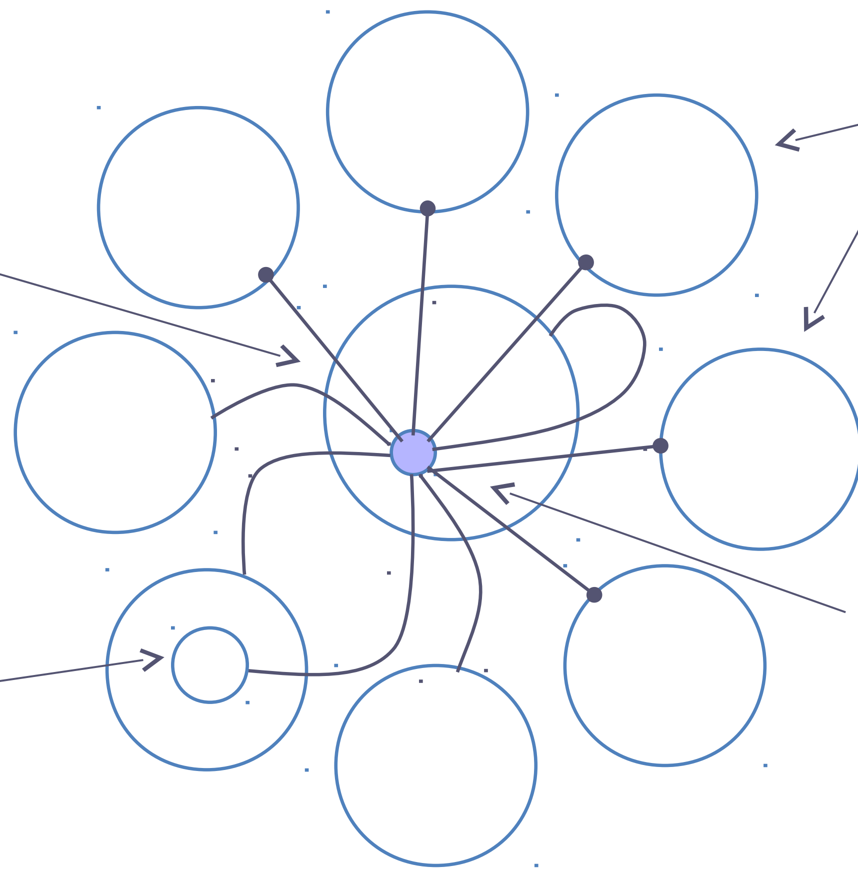
Modular Networks
Experimental Setup 1

- In these trials there are eight modules of 100 excitatory neurons each, plus 200 inhibitory neurons
- Each module has 1000 randomly assigned one-way excitatory-to-excitatory connections (before the rewiring phase)
- Note that connections are *not* symmetrical, so we have a directed network
- Connections from excitatory to inhibitory neurons are *focal*, not diffuse. Each inhibitory neuron has connections from four excitatory neurons (all within the same module)
- Inhibitory connections are diffuse. Each inhibitory neuron projects to all excitatory and inhibitory neurons (in all modules)

Modular Networks
Experimental Setup 2

200 inhibitory neurons

100 excitatory neurons per module



Four excitatory neurons (all from the same module) project to each inhibitory neuron

Each inhibitory neuron projects to every neuron in the whole network (but receives input from just four excitatory neurons)

Modular Networks
Experimental Setup 3

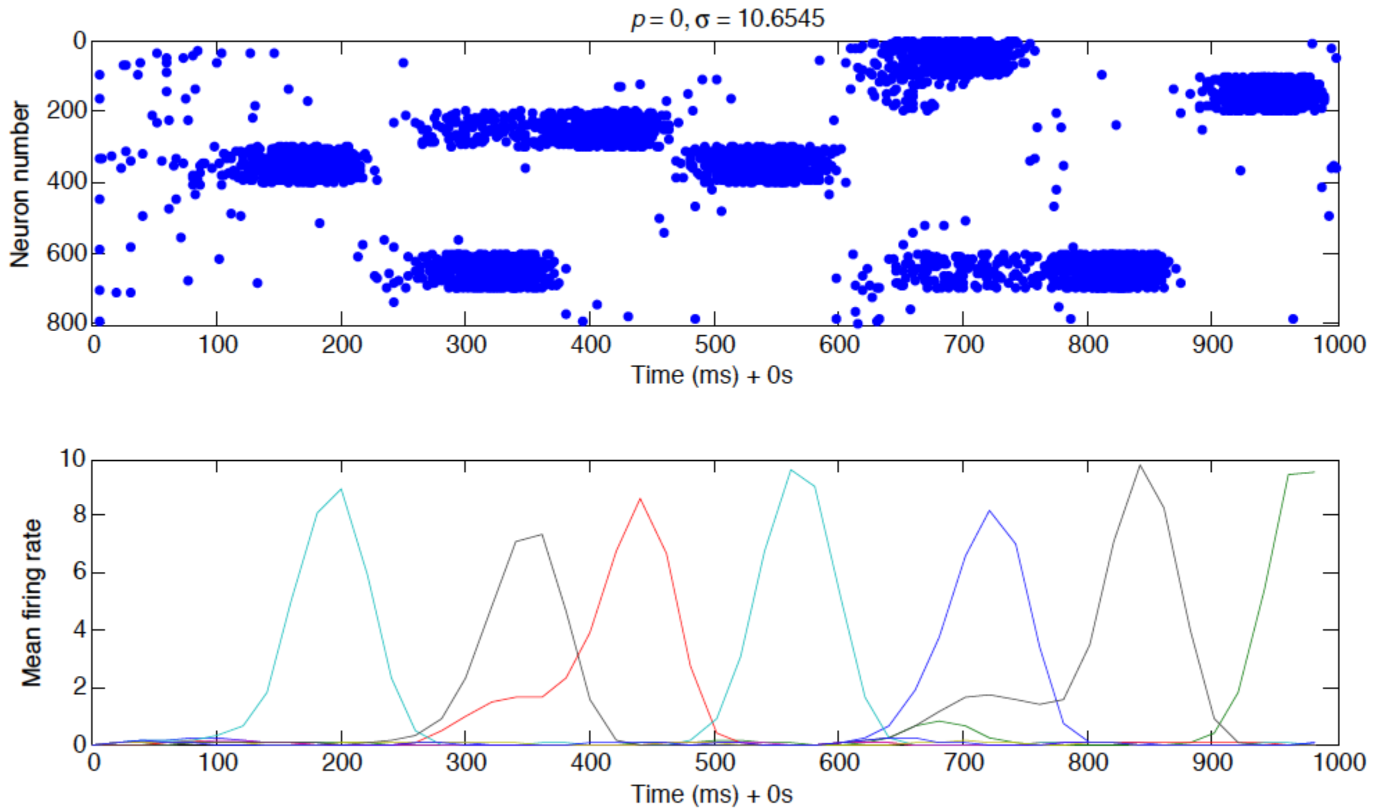
- There is a spread of conduction delays in the excitatory to excitatory connections. The rest of the connections have a conduction delay of one, so that inhibition can act fast
- To compensate for the fact that focal connections give rise to fewer incoming excitatory connections to an inhibitory neuron than in the diffuse case, the scaling factor of these excitatory to inhibitory connections is set high (to 50)
- There is a small amount of background firing to prevent activation from dying out. This is generated by a Poisson process with $\lambda = 0.01$ for each neuron at every 1ms. When this process produces a value > 0, extra current (I=15) is injected into the neuron, causing occasional spontaneous firing

Modular Networks
Experimental Setup 4

	Weight	*Scaling factor*	*Projection pattern*	*Conduction delay*
Excitatory-excitatory	1	17	Modular small-world	Random 1ms to 20ms
Excitatory-inhibitory	Random 0 to 1	50	Focal from module	1ms
Inhibitory-excitatory	Random -1 to 0	2	Diffuse to whole network	1ms
Inhibitory-inhibitory	Random -1 to 0	1	Diffuse to whole network	1ms

Modular Networks 1

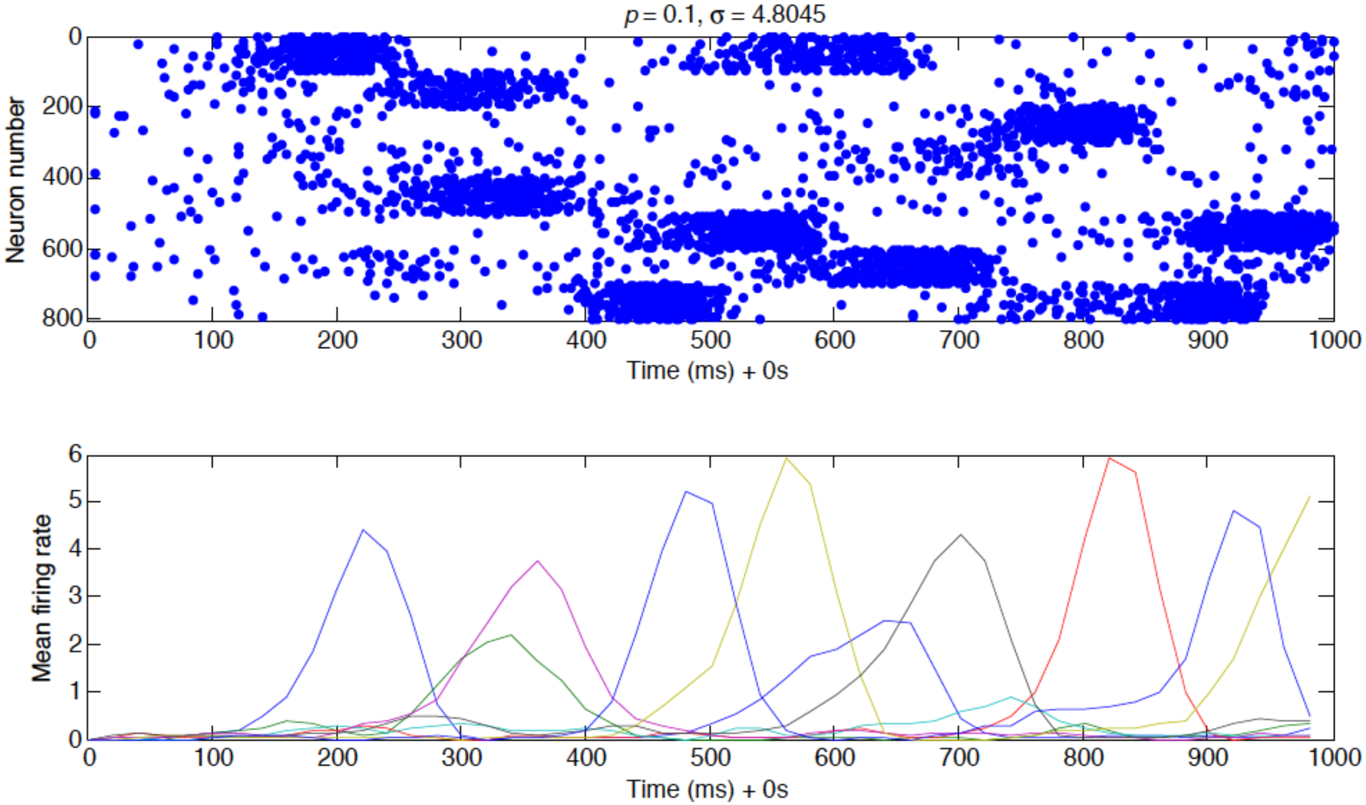
- With p = 0, each module behaves independently



p = 0

Modular Networks 2

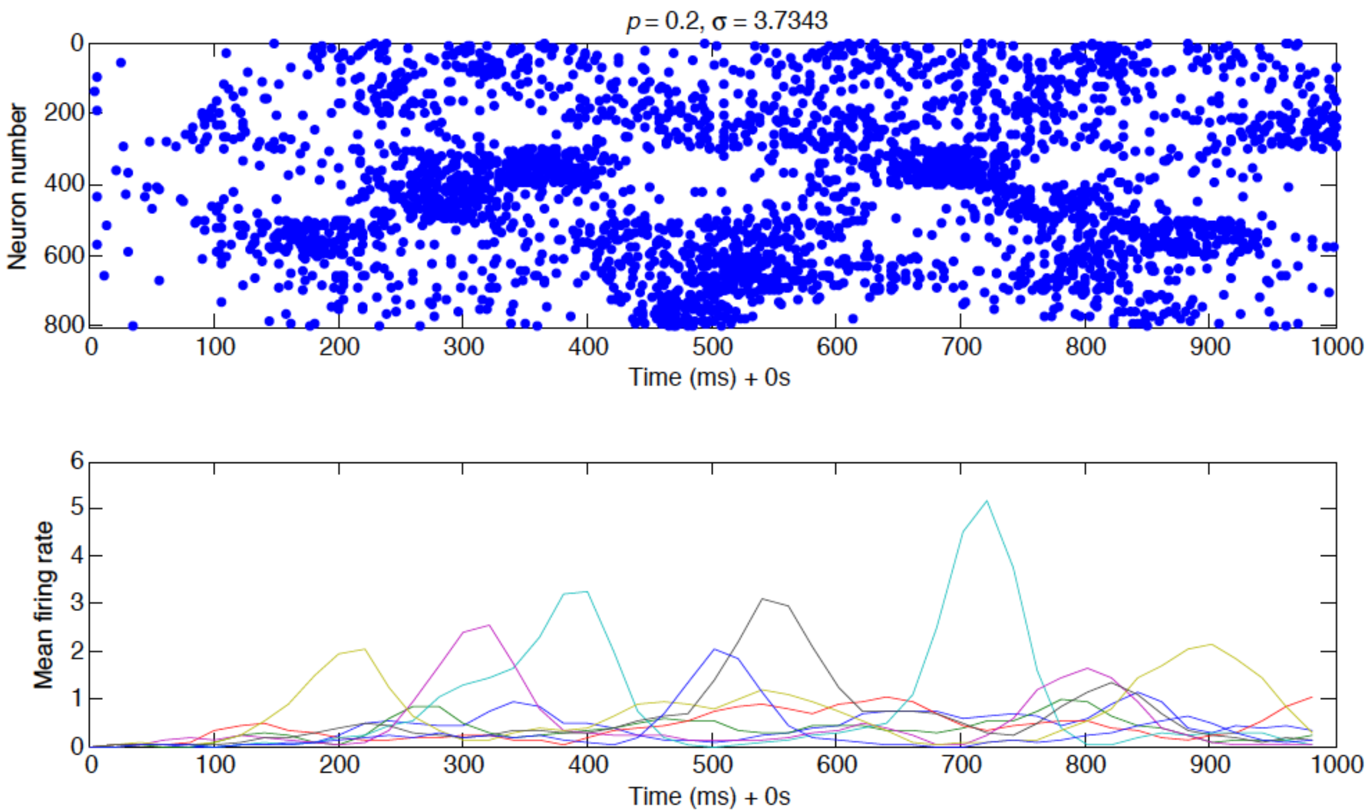
- With p = 0.1, the modules are exercising some influence on each other, but still behaving largely independently



p = 0.1

Modular Networks 3

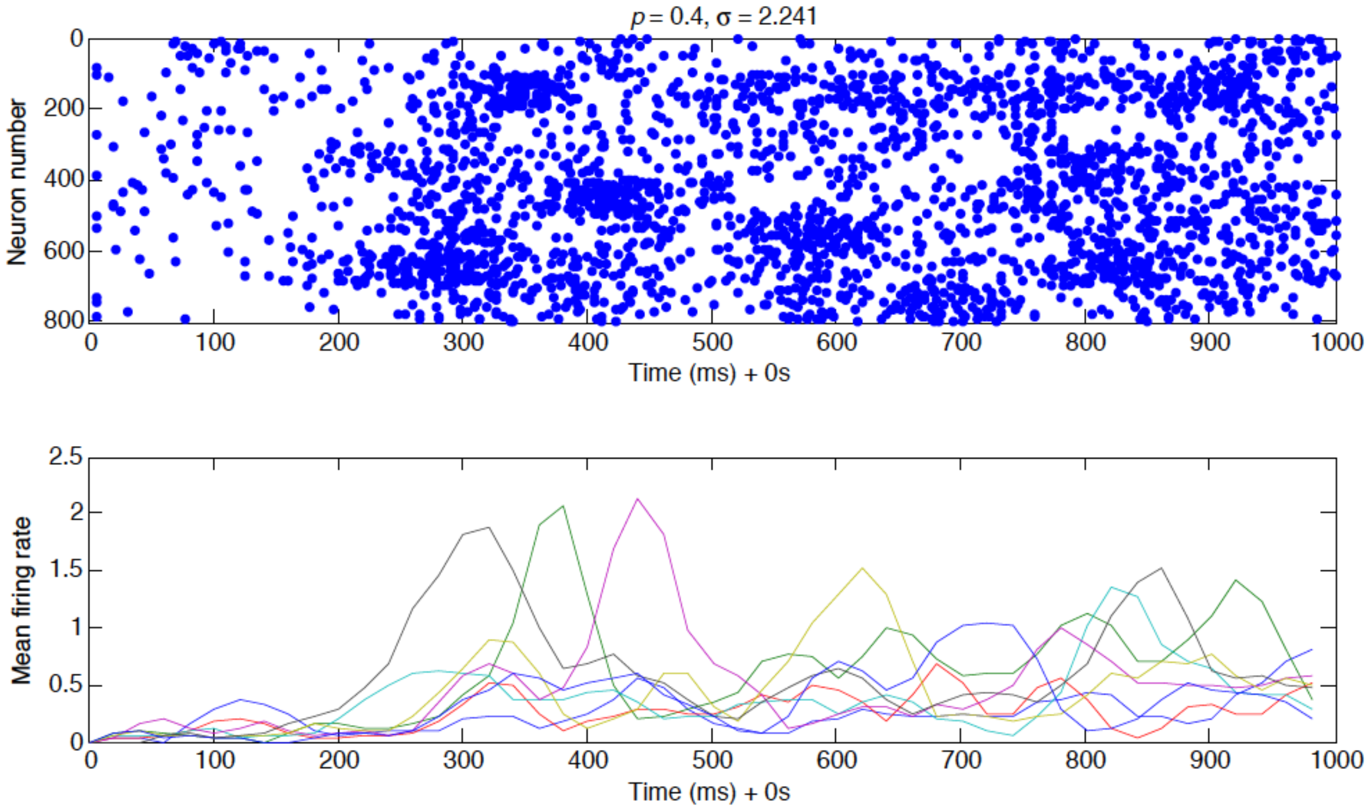
- With p = 0.2, the influence between modules is greater



p = 0.2

Modular Networks 4

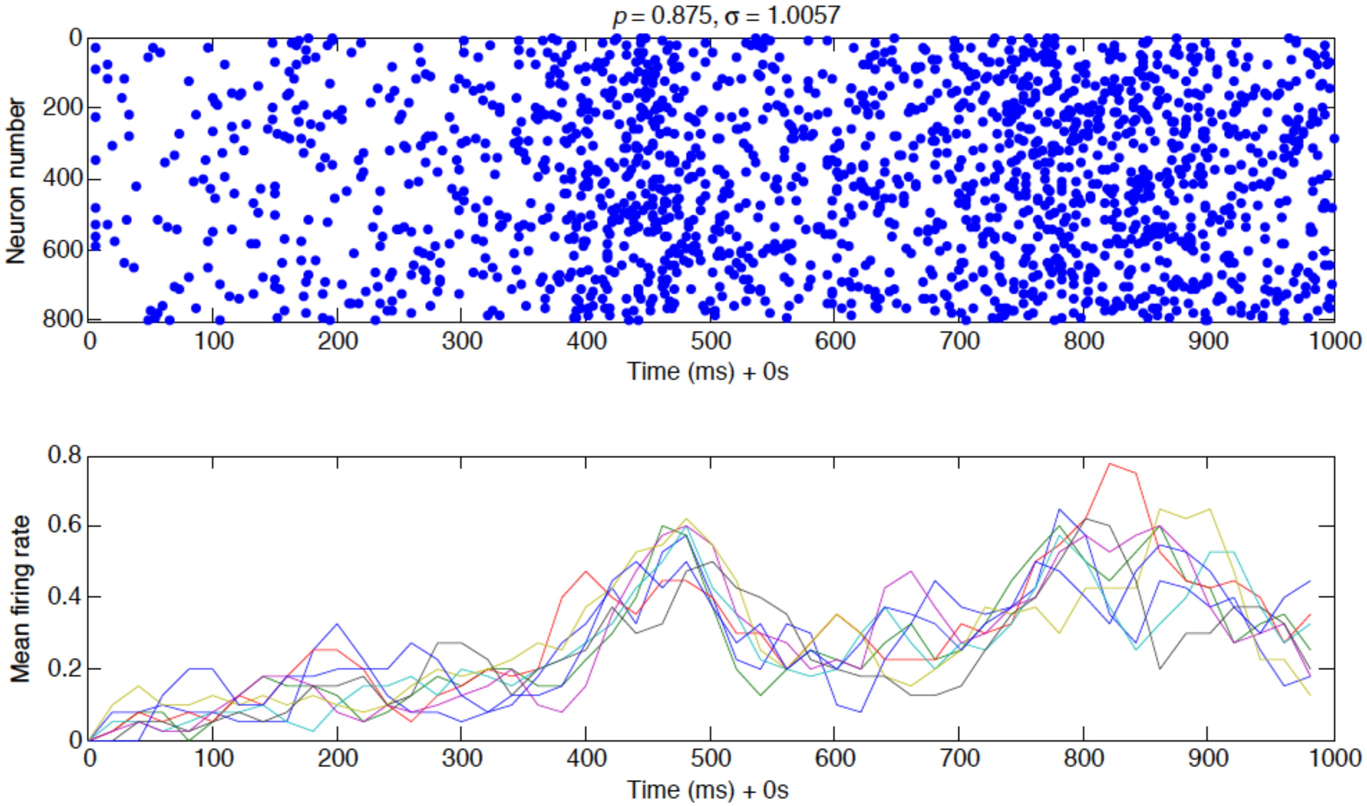
- With p = 0.4, evidence of independent activity is diminishing



p = 0.4

Modular Networks 5

- If p = 0.875 (7/8) we have a random network, and the modules have gone



p = 7/8

Spatial Embedding

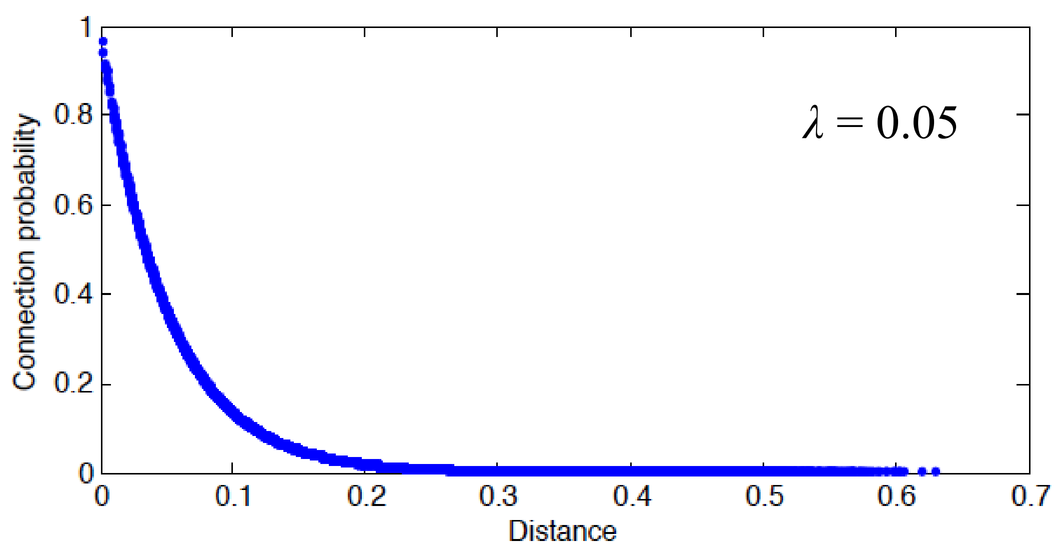
- Real networks, including brain networks, are often *spatially embedded*. This means the nodes have some spatial location, and the spatial locations of nodes influences their connectivity
- The ring lattice in the Watts-Strogatz procedure is one sort of spatial embedding. But it's only one-dimensional, and the distances are discrete rather than continuous
- A more realistic embedding results from assigning each node a location on a 2D plane
- By making the probability of connection depend on distance, we can construct another type of realistic network with a high small-world index, and medium to high modularity
- This is not such a good model of whole-brain connectivity, but it is a good model of a small patch of cortex

2D Small World Networks 1

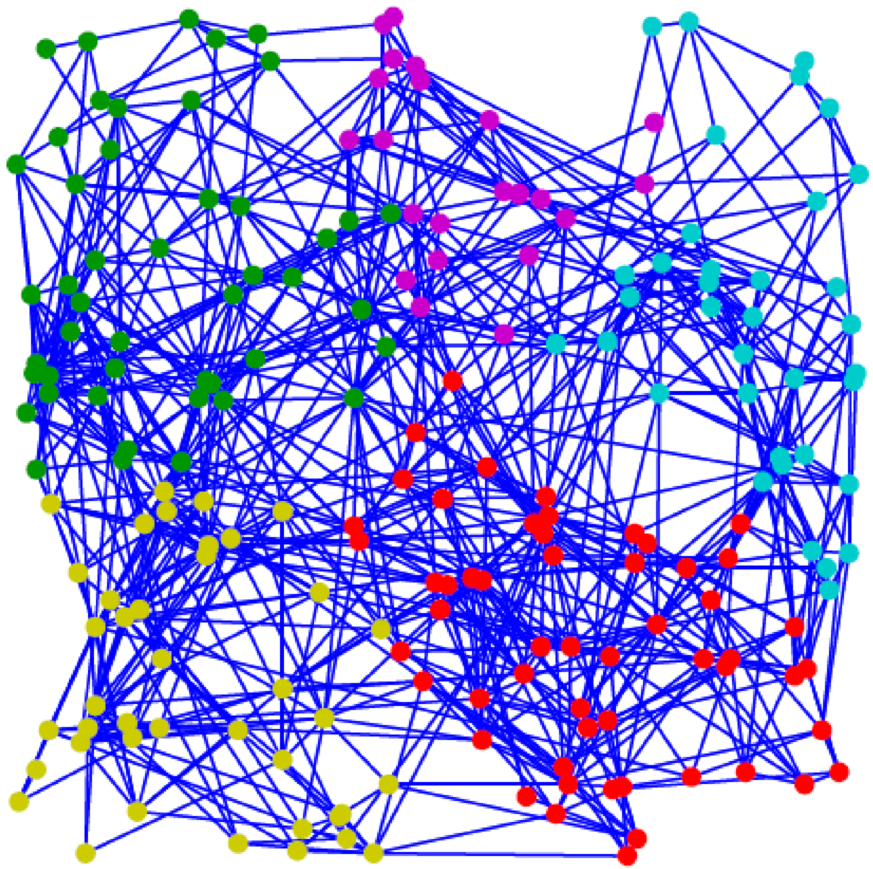
- Suppose that neurons are arranged on a 2D square, and each is assigned random coordinates in the range 0 to 1. This ensures that the distance between any two nodes is in the range 0 to $\sqrt{2}$
- Then let the probability p of a connection between any two nodes be

$$p = e^{-d/\lambda}$$

where d is the distance between the nodes and λ is the synaptic lengthscale



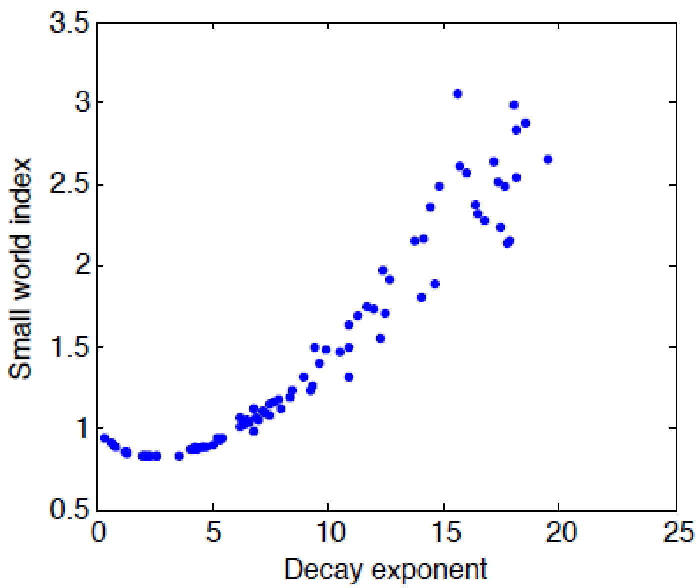
2D Small World Networks 2

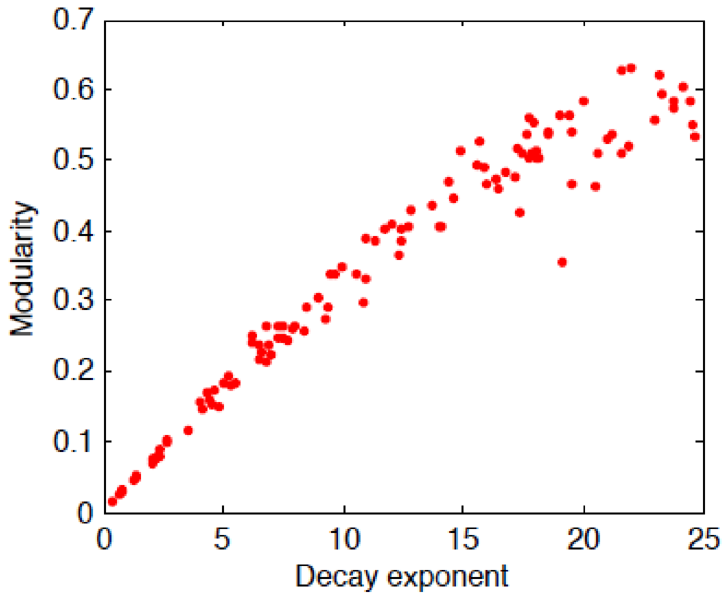


- Here's an example of a spatially embedded network generated in this way, with 200 nodes and $\lambda = 0.05$
- The small world index is 2.8585, which is fairly high
- The network is also quite modular. The colours are an assignment of nodes to modules, giving Q=0.5195

2D Small-World Networks 3

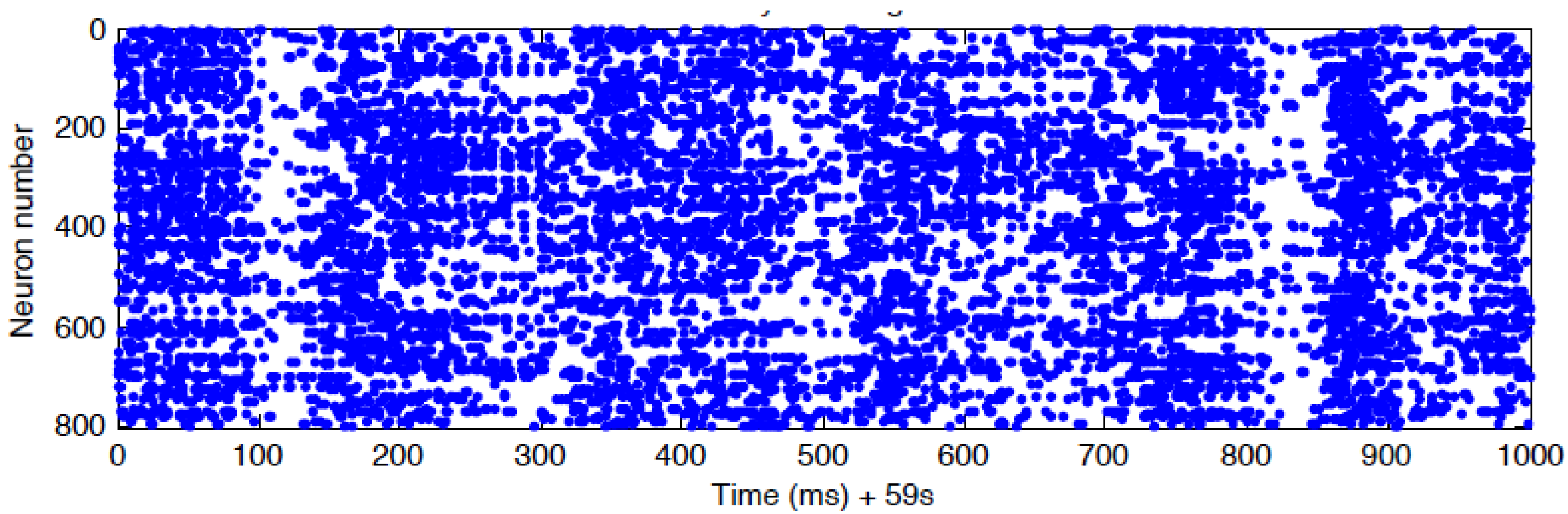
- If we randomly generate spatially embedded networks (with 100 nodes) we find that both small-world index and modularity increase with the decay exponent $h = \lambda^{-1}$
- But with very high h, the network fragments (becomes disconnected), and the small-world index is undefined





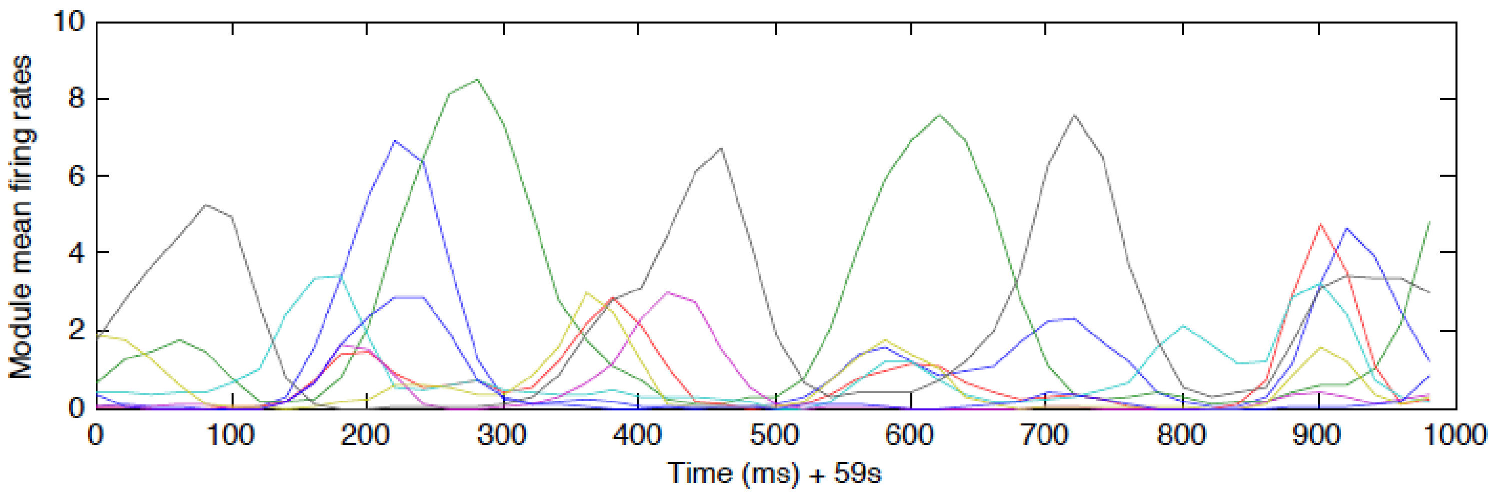
Spatial Embedding 1

- We can also study the dynamical complexity of spatially-embedded small-world neural networks
- These exhibit a rich variety of phenomena, which are evident from inspection of the raster plot



Spatial Embedding 2

- To get a better idea of what's going on here, we can extract the modular structure of a spatially embedded network. That is, we find a partitioning of the network into modules that yields a high value for Q
- Then, we examine the mean firing rates in the n largest modules. Here we see the results for n = 8 for the (typical) trial on the previous slide
- It is noteworthy that the extracted modules exhibit independent, periodic behaviour



Dynamical Complexity

- In the brain, the complex dynamical regime is thought to underlie high-level cognition, and perhaps consciousness (Tononi, Edelman & Sporns 1998)
- Dynamical complexity can be thought of as a balance between *segregated* and *integrated* activity
  - An overly integrated system is frozen and incapable of a large repertoire of differentiated responses
  - An overly segregated system cannot orchestrate its resources to provide a unified response to the ongoing situation
- But how to assess dynamical complexity is still unclear. We'll get to that in a sec

Quantifying Complexity

- Dynamical complexity has a loose definition, and can be interpreted in many ways.
- It is often described as a balance between competing phenomena: chaos/synchrony, segregation/integration, order/disorder.
- However there is no clear-cut definition on what dynamical complexity means or how to quantify it in a rigorous way.
- We will explore two different mathematical tools to reason about and quantify complexity:
  - Dynamical Systems Theory
  - Information Theory

Dynamical Systems Theory

- DST studies neurons as *dynamical systems*: sets of variables and equations that determine the state and evolution of the (neural) system.
- Most methods rely on inspecting the trajectories of the system in its *state-space*, the space of all its possible configurations.
- State-space properties:
    - Attractors
    - Bifurcations
    - Limit cycles
- Large-scale dynamic phenomena:
    - Lyapunov stability (i.e. critical exponents)
    - Spectral methods
    - Phase transitions and **criticality**

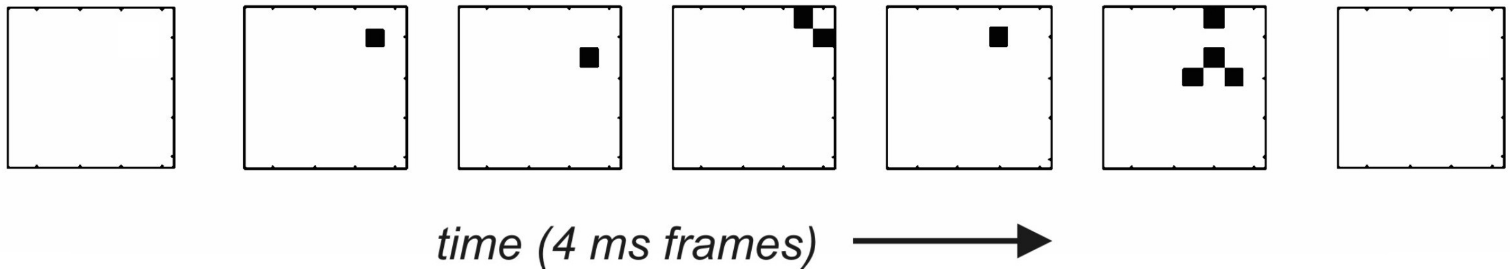
Criticality

- A system is said to be *critical* if it is poised between order and disorder
- Criticality is associated with high dynamical complexity:
  - Highly segregated activity is highly disordered (e.g. no synchronisation), therefore low dynamical complexity
  - Highly integrated activity is highly ordered (e.g. complete synchronisation), therefore of low dynamical complexity
  - If the system is poised between order and disorder then there is a balance of integration and segregation (eg: fluctuating coalitions of synchronised processes)

- Often critical dynamics occur in a narrow range of some parameter (e.g. rewiring probability), with order on one side and disorder on the other --- a phase transition.

Neuronal Avalanches 1

- A natural way to study large-scale dynamics is to look at what patterns neurons follow when they fire together.
- Neuronal avalanches are an example.
- It was shown by Beggs & Plenz (2003) that neurons in a culture fire avalanches of spikes.

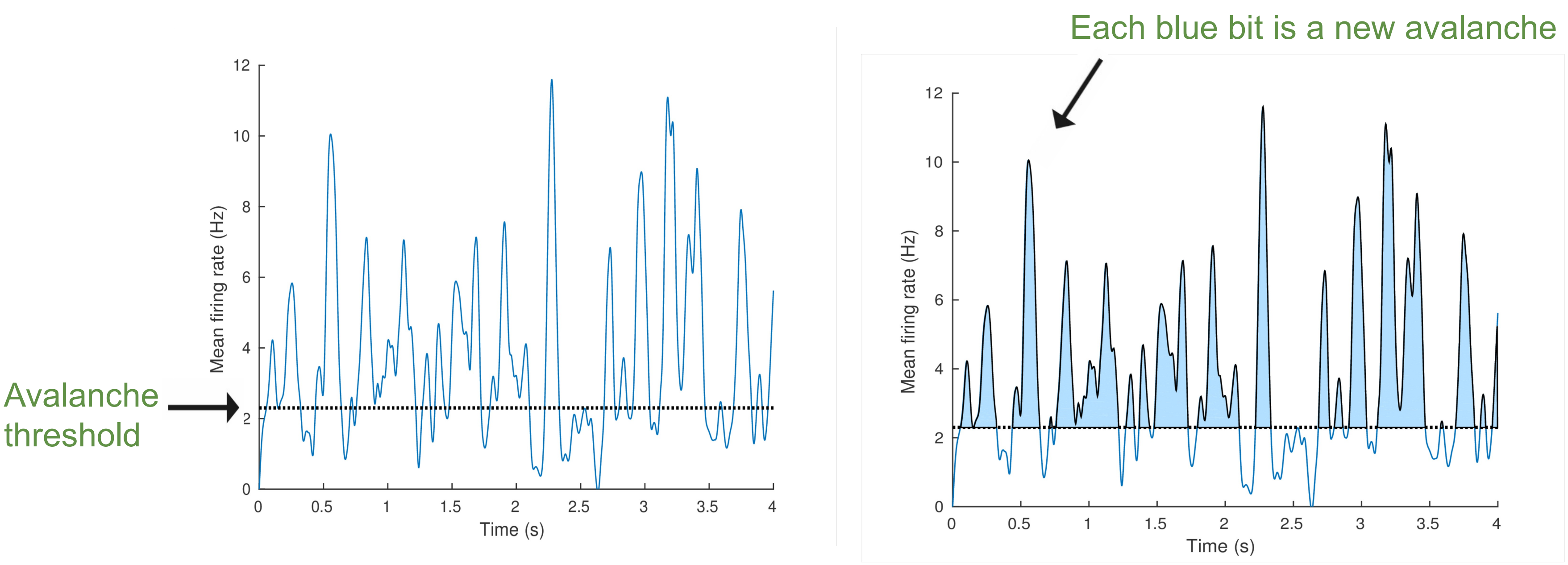


A neuronal avalanche of size 9 spikes recorded on a square array of electrodes

From *Scholarpedia*

Neuronal Avalanches 2

- To extract avalanches from a neural recording we search for periods of *uninterrupted activity*.
- The sizes of these avalanches are gathered in the *avalanche-size distribution*, an informative tool to study large-scale dynamic behaviour.

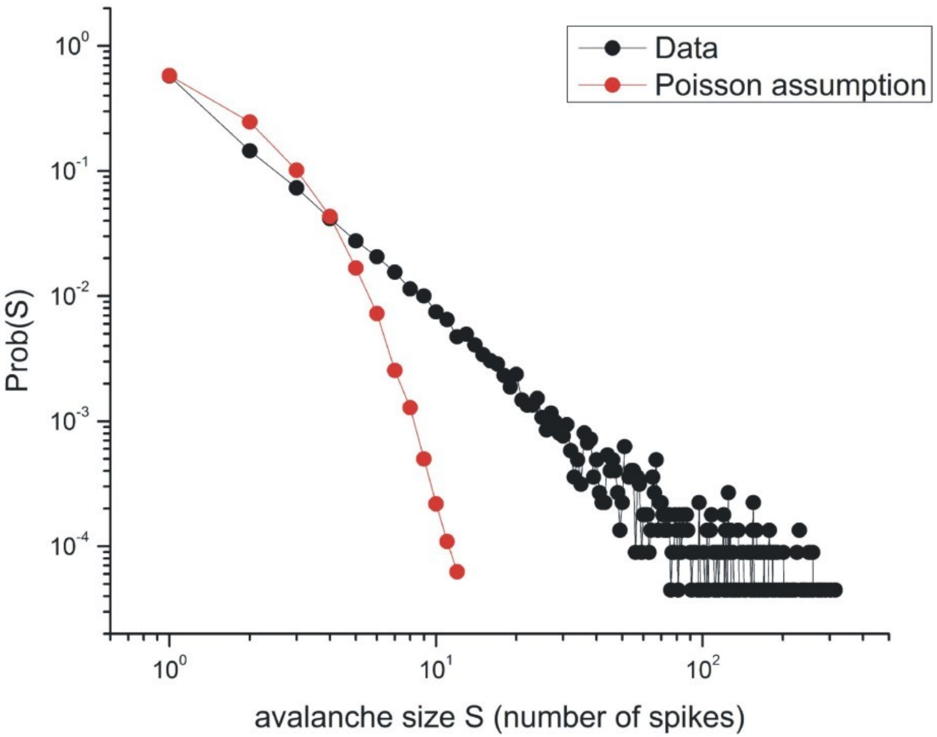


Avalanche Distributions 1

- In real neurons, the sizes of the avalanches follow a *power law*, the signature of critical behaviour

$$P(s) = \frac{1}{Z} s^{-\alpha}$$

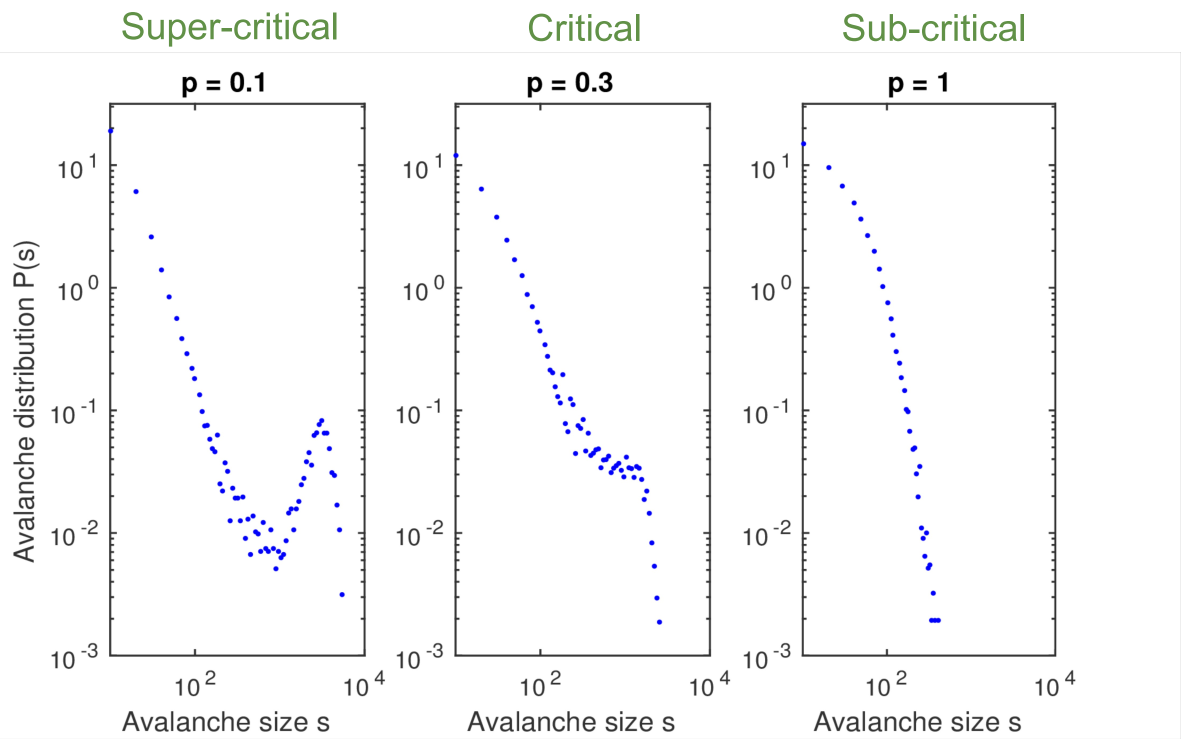
- When the avalanche size if plotted against frequency on a log-log scale, we get a straight line (up to the size of the system) with a critical exponent of α = -1.5



From *Scholarpedia*

Avalanche Distributions 2

- The modular network exhibits a transition from an ordered regime to a disordered regime, encountering a critical state in-between.



(Mediano & Shanahan, in prep.)

Information Theory

- Originally developed for encrypted warfare communications.
- All phenomena in any system are reduced to *bits*, the universal unit of information.
- We say that information is *substrate-independent*.
- IT operates on *probability distributions*, i.e. characterises all phenomena in their specific context.
  - Dust off your statistics textbook.
- The information or "surprise" obtained when observing an event with probability *p*

$$i(p) = -\log(p)$$

Entropy

- Let a variable *X* have a set of possible states Ω_X
- The states in Ω don't need to be the physical state of the system --- any *informational state* extracted from it will work.
- The *entropy H* is the building block of the whole IT.
- Intuitively, H is a measure of how much information can be carried in X:
  - If X is always the same then it can't carry information
  - If X takes on each of its possible states equally often then it can carry the maximum amount of information

$$H(X) = -\sum_{x \in \Omega} p(x) \log_2 p(x)$$

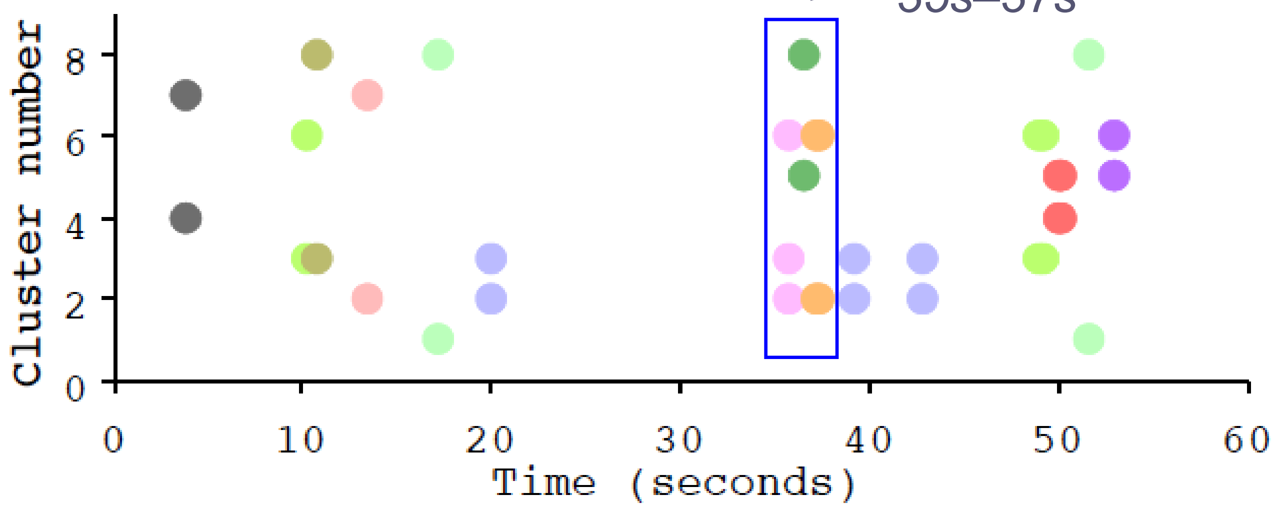
Coalition Entropy

- We can use entropy to quantify the size of the repertoire of distinct states a system can visit
- The *coalition entropy* H_C of a system is defined as the entropy of the coalition configurations visited by the system
- In this case, the coalitions form the information states Ω_X of the previous slide. That means we only care about the information contained in the coalition configuration.
- Intuitively, a coalition is a group of neural processes that are simultaneously active and influencing each other
- More mathematically, a set of neural populations form a coalition if their activity waxes and wanes *in synchrony*
- We'll cover how coalitions emerge and how to find them in Topics 10 and 11

Coalitions in Small-World Networks

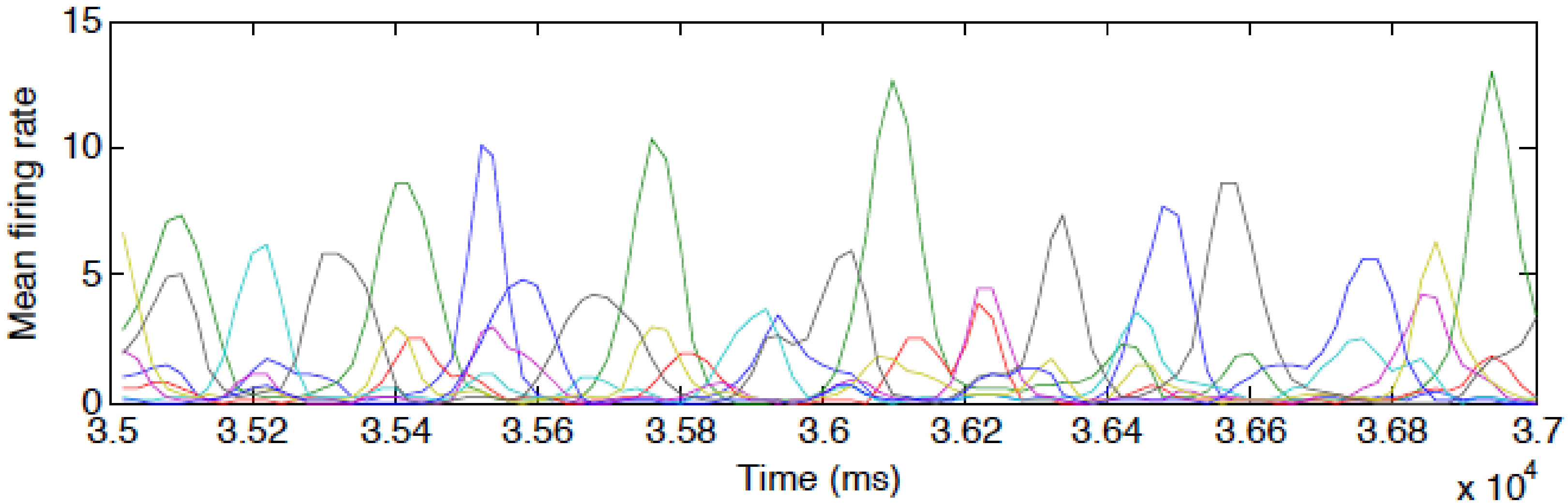
- Here is a plot of the coalitions formed during a 60 second run of the modular small-world network
- Each colour represents a distinct coalition, that is to say a combination of modules

Let's consider this period, from 35s–37s



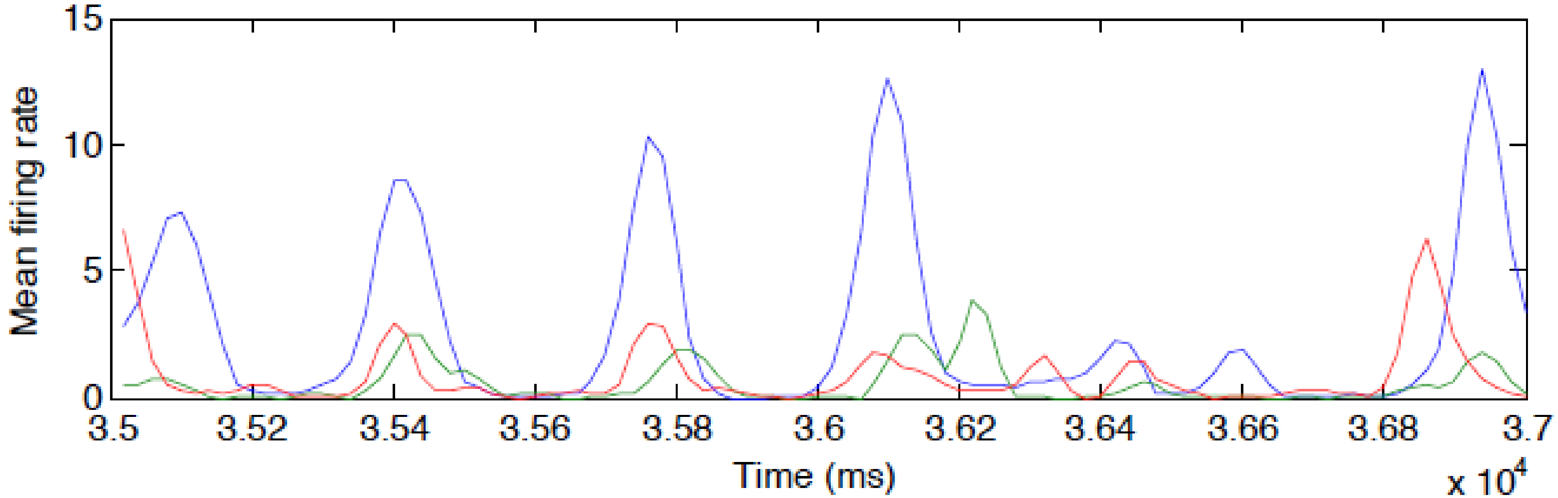
Coalitions in Small-World Networks 2

- Activity during the selected period is a mess, although it shows some signs of periodicity
- So let's isolate the first coalition indicated on the previous slide



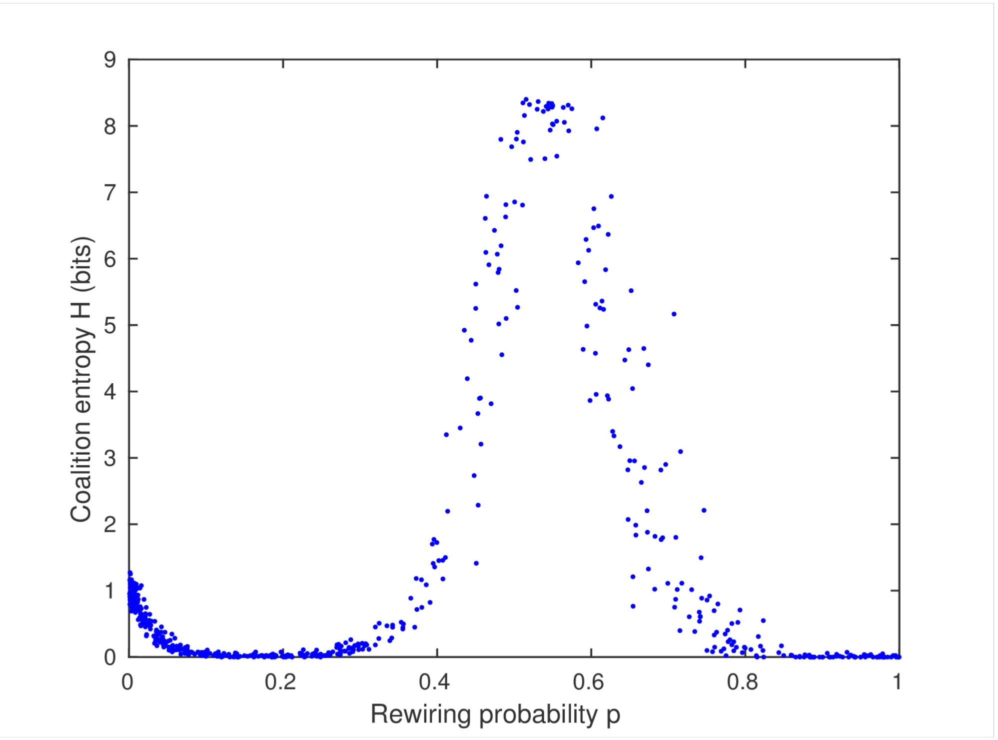
Coalitions in Small-World Networks 3

- This is the activity in modules 2, 3, and 6
- It's clear that these modules are well synchronised, especially between 35.2s and 36.2s



Coalition Entropy

- On its own, entropy quantifies disorder (i.e. is maximal for a highly segregated system). But neural populations don't synchronise if they're doing separate things.
- By chosing an appropriate informational state we have turned a disorder measure into something more sophisticated



Conditional Entropy

- To introduce interactions between the variables we use *conditional* probability distributions.
- This is akin to reasoning about *X* after observing *Y*.
- *H(X|Y)* is the expected entropy of *X* after *Y* is known.
- For example, if *H(X|Y) = H(X)* then X and Y are independent.
- Most information-theoretic measures can be easily understood in terms of entropy and conditional entropy.

$$H(X|Y) = \sum_{y} p(y) H(X|y) = -\sum_{x,y} p(x,y) \log_2 p(x|y)$$

Conditional Entropy 2

- In neuroscience it is typically used to characterise stimulus-response relations.
- H(R) is the entropy of a neural response, H(R|S) is the entropy of the same population given the stimulus
  - If H(R) is high, the population either is very noisy or carries a lot of information
  - If H(R|S) is low, the population is highly selective to the stimulus
  - If H(R|S) is still high, the population does not have information about S.

Mutual Information

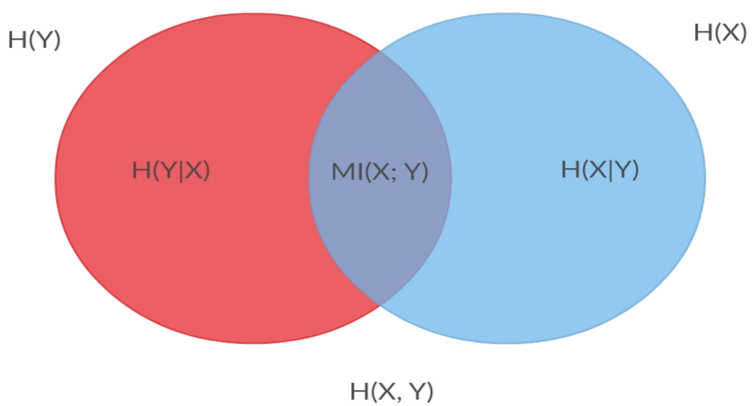
- The *mutual information* $\mathrm{MI}(X;Y)$ between two variables X and Y is a measure of how much information there is in X about Y and vice versa.
- In other words, how much does knowing Y reduce the uncertainty of X.

$$\begin{aligned}\mathrm{MI}(X;Y) &= H(X) - H(X|Y)\\ &= H(X) + H(Y) - H(X,Y)\end{aligned}$$

- In a neural context, it's useful to quantify how much information a population has about:
  - Other populations
  - An external stimulus

Mutual Information 2

- Can be visualised with a Venn diagram
- Also useful to visualise other quantities, like *joint entropy* H(X,Y)



Conditional Mutual Information

- Similarly, the *conditional mutual information* $\mathrm{MI}(X; Y| Z)$ is how much information X and Y share after the influence of Z has been taken into account.
- It's easily defined with the previous definition of MI and conditional entropy:

$$\mathrm{MI}(X; Y | Z) = H(X | Z) - H(X | Y, Z)$$

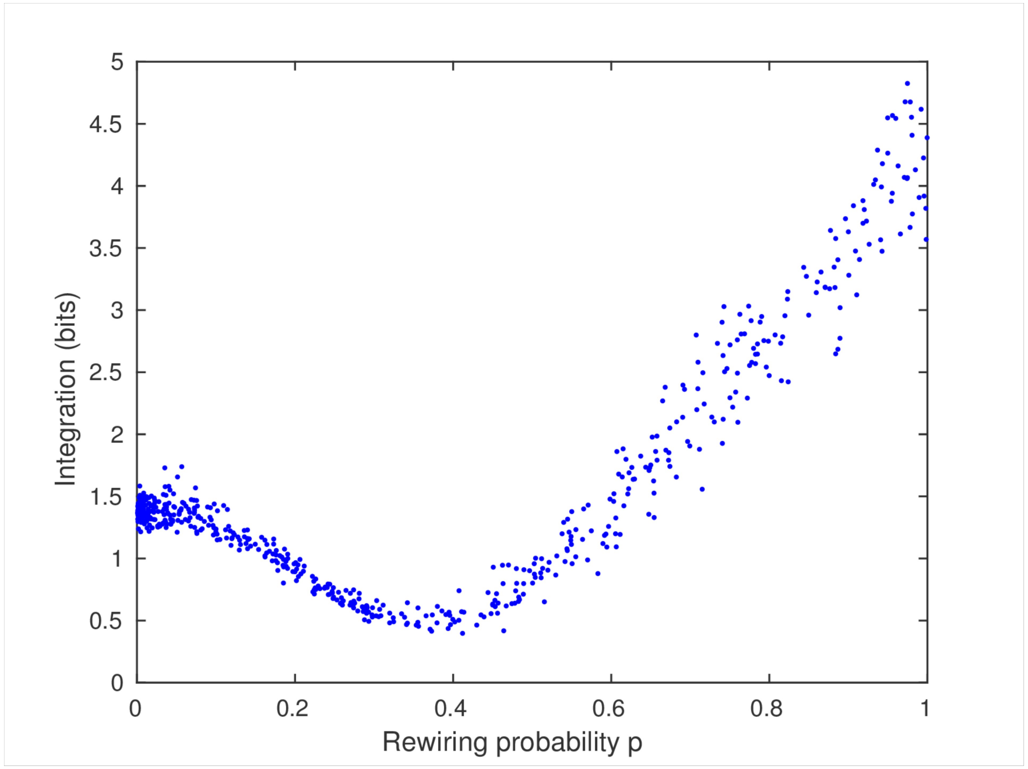
Integration

- Integration (or *multi-information*) is a possible extension of MI to multivariate settings.
- The integration $I(S)$ of a system S with parts X_i is the difference between the entropy of all the individual components and the entropy of the system as a whole
- In other words, how much entropy do the individual components of the system have that isn't accounted for by the entropy of the overall system
- If all the components of the system are doing the same thing, then the system is too integrated to have high dynamical complexity

$$I(S)=\left(\sum_{i=1}^{n} H(X_i)\right)-H(S)$$

Integration 2

- In the modular network, integration peaks downwards
- I(S) is non-zero for p = 0 because modules interact indirectly through the inhibition
- On the left, modules fully compete, on the right they fully cooperate – it's in the middle where they lose track of each other



Neural Complexity

- Quantifies complexity by inspecting the system at all scales
  - Suggested initially by Tononi, Edelman, and Sporns
- Measures the extent to which there are independent interactions between the the parts of a system and the whole

Average over all partitions of size *k*

$$C(S)=\sum_{k=1}^{n}\left(\frac{k}{n}I(S)-\langle I(X^{k})\rangle\right)$$

- If the system is too integrated, the first terms of the sum will be high, but the rest will be small, resulting in a low overall value.
- Unfortunately the modular net is too small to see meaningful neural complexity

Diachronic Complexity

- So far we've seen *synchronic* measures of integration and segregation in a system. They look at instantaneous snapshots of the system. On a temporal dimension they are only concerned with the statistics of these snapshots.
- We also need time-directed measures of complexity that provide a *dynamic account of information processing*.
- *Transfer entropy* is an alternative measure of dynamical complexity.
- Rather than looking at instantaneous snapshots of a system, it looks for influences between the components of the system *diachronically*, that is to say over time

Transfer Entropy

- Quantifies *predictive information flow* between parts of the system.
- Formulated in terms of mutual information:

$$TE(X \rightarrow Y) = MI\left(X(t\text{-}1), Y(t) \mid Y(t\text{-}1)\right)$$

- How good is X at predicting Y, over and above the level that Y predicts itself?
- It does NOT mean that X causes Y! Assessing causality requires very sophisticated tools.

Transfer Entropy 2

- In IT terminology, we say the *X* is the *source* and *Y* is the *target*.
- TE can be understood with conditional entropy

$$TE(X \rightarrow Y) = H(Y(t)|Y(t\text{-}1)) - H(Y(t)|X(t\text{-}1), Y(t\text{-}1))$$

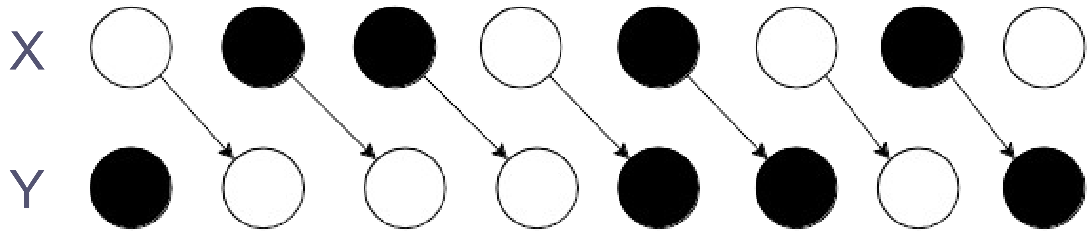
- We can also define conditional transfer entropy – how much does *X* help predicting *Y* above *Y*'s *and Z*'s past.

$$TE(X \rightarrow Y|Z) = MI(X(t\text{-}1), Y(t)|\ Y(t\text{-}1), Z(t\text{-}1))$$

- Doesn't need to be between *t* and *t-1*, {*X, Y, Z*} can have arbitrary *delay embeddings*.

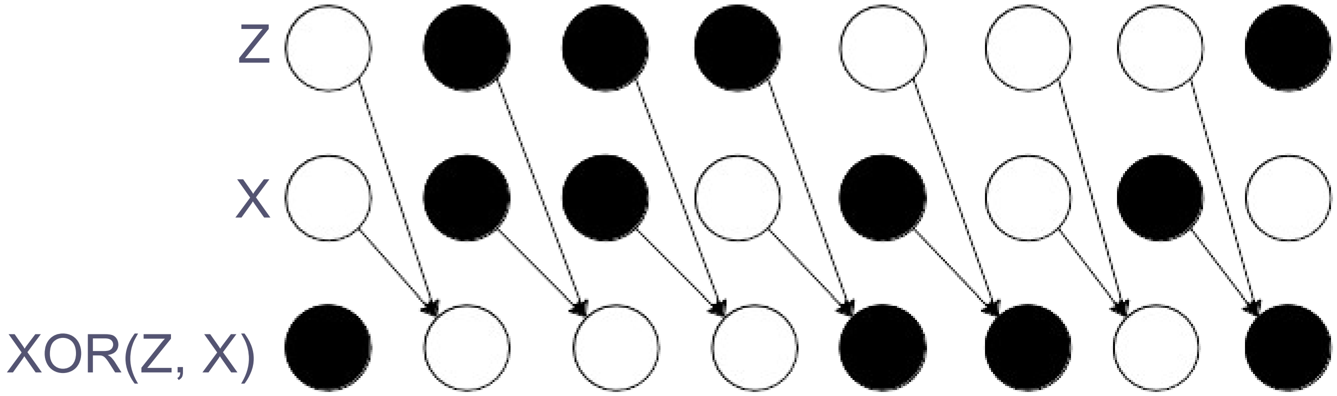
Transfer Entropy Example

- Overly simplistic use of TE can bring misleading results.
- *Y* seems random, so it can't predict itself – i.e. H(Y(t)| Y(t-1)) is large
- But it is uncorrelated with *X*, so H(Y(t) | Y(t-1), X(t-1)) is also large
- In this example, TE from X to Y is very small.



Transfer Entropy Example

- TE from the joint system {X,Z} to Y is very large.
- Combining information in X and a hidden source Z we obtain much more predictive power over Y. We say that the sources X,Z have *synergistic information* about Y.
- New branch of IT deals with these issues: *Partial Information Decomposition*.



Causal Density 1

- Conditional transfer entropy assesses the influence of one variable (X) on another (Y) *over and above the influence of the rest of the system* (Z)
- This can be generalised to *multivariate* time series, whose *causal density* is then

$$CD(S) = \frac{1}{n(n-1)} \sum_{i,j} TE(X_i \rightarrow X_j | Z)$$

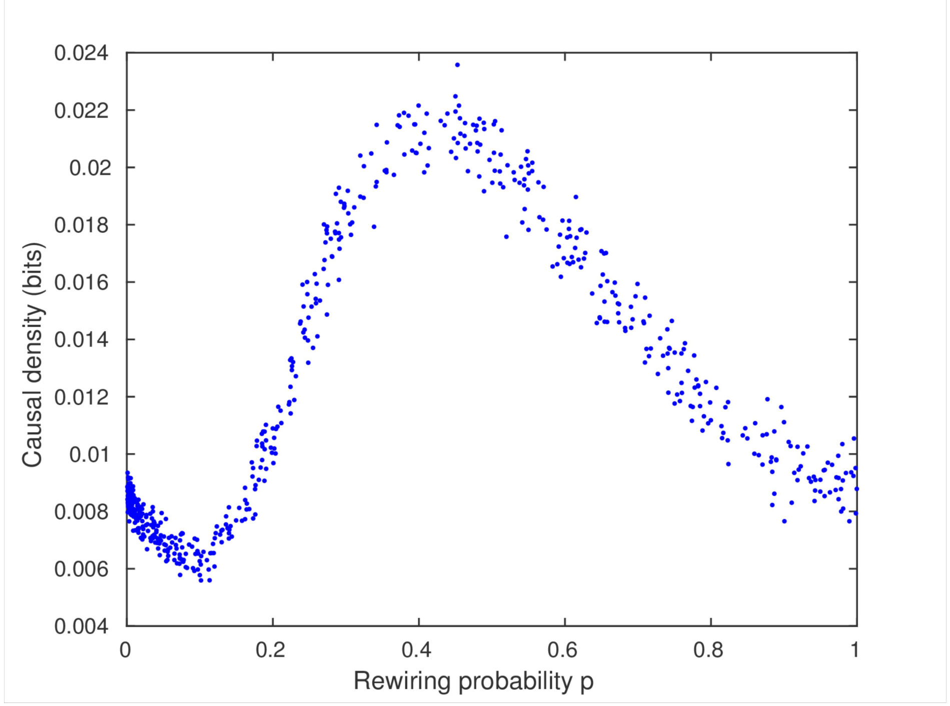
where Z is everything else apart from X_i and X_j

Causal Density 2

- Causal density quantifies the balance of segregated and integrated activity in a system
- If activity is highly segregated, causal density will be low because variables will not exercise influence on each other
- If activity is highly integrated, causal density will be low because variables will not exercise influence on each other over and above the influence of the rest of the system
- This adds a temporal component to the notion of complexity: not only its state must be complex but also its evolution
- In the modular network the modular division provides a natural partition of the system

Causal Density 3

- Causal density peaks at around $p = 0.4$, suggesting a high dynamical complexity
- This is the region where behaviour is most critical!
- Critical dynamics supports increased communication between the modules



A Zoo of Estimators

- All the maths we've seen above are valid for *discrete* variables. Changing the maths is easy – replace sums with integrals.
- In practice, information-theoretic quantities are hard to estimate from experimental or simulated data.
- We'll use a toolkit to make our lives easier.
- The *Java Information Dynamics Toolkit* (JIDT) by J. Lizier is highly recommended.

http://jlizier.github.io/jidt/

JIDT

And many more!

- IT offers a principled way to formulate new measures.
- Understanding how they perform in practical contexts is much harder, though.
- New measures are being developed, and information-based complexity studies are an emerging trend:
  - Multivariate transfer entropy
  - Integrated information (Φ)
  - Partial information decomposition
- Understanding the connection between dynamical and informational measures of complexity is a major challenge in neuroscience

Related Reading 1

Roxin, A., Riecke, H. & Solla, S.A. (2004). Self-Sustained Activity in a Small-World Network of Excitable Neurons. *Physical Review Letters* 92 (19), 198101.

Seth, A.K., Izhikevich, E.M., Reeke, G.N and Edelman, G.M. (2006). Theories and Measures of Consciousness: An Extended Framework. *Proc. Natl. Acad. Sci. USA* 103, 10799.

Shanahan, M.P. (2008). Dynamical Complexity in Small-World Networks of Spiking Neurons. *Physical Review E*, 041924.

Beggs, J. & Plenz, D. (2003). Neuronal Avalanches in Neocortical Circuits. *Journal of Neuroscience* 23(35), 11167–11177

Related Reading 2

Tononi, G., Edelman, G.M & Sporns, O. (1998). Complexity and Coherency: Integrating Information in the Brain. *Trends in Cognitive Sciences* 2(12), 474–484.

Seth, A.K., Barrett, A.B. & Barnett, L. (2011). Causal Density and Integrated Information as Measures of Conscious Level. *Philosophical Transactions of the Royal Society A* 369, 3748–3767.

Wibral, M., Vicente, R. and Lizier, J. (2014). Directed Information Measures in Neuroscience. *Springer Berlin* . ISBN: 978-3-642-54473-6