Firefly Synchronization

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Biological Inspiration

- Why do fireflies flash?
  - Mating purposes
    - Males flash to attract the attention of nearby females

- Why do fireflies synchronize their flashes?
  - Help females recognize the flashes of conspecific males?
  - A result of competition between males?
  - In response to certain "pacemaker" fireflies?

Generalizations and Further Motivations

- Fireflies as paradigm for other coupled biological oscillators
  - Pacemaker cells in heart
  - Neurons
  - Circadian Pacemakers (24 cycle)
  - Crickets chirping
  - Insulin-secreting cells in pancreas
  - Womens' menstrual cycles

Dynamics of Synchrony

- Three routes to synchrony in fireflies:
  - Phase Advancing
    - Firefly only advances phase ("integrate and fire")
    - *Photinus pyralis*; transient synchrony
  - Phase Delaying
    - Firefly flash is inhibited by neighbor flash; phase may advance or delay.
    - Observed in *P. cribellata*; many possible frequencies
  - Perfect Synchrony
    - Can entrain with zero phase lag, even with different intrinsic/stimulus frequencies
    - Observed in *P. malaccae*, *Pteroptyx tener*, and *Luciola pupilla*

Question

How do coupling strength and number of neighbors within visual range affect the time until synchronization for a population of fireflies?

Mathematical Models for Fireflies

- Many mathematical models exist for modelling firefly dynamics
  - Strogatz: Globally coupled integrate and fire pacemaker model
  - Kuramoto: Globally coupled, phases dynamics determined by neighbor average
  - Avila: Biologically inspired

Kuramoto Model

$$\frac{d\theta_i}{dt} = \omega_t + \frac{K}{N}\sum_{j=1}^{N}\sin(\theta_j - \theta_i)$$

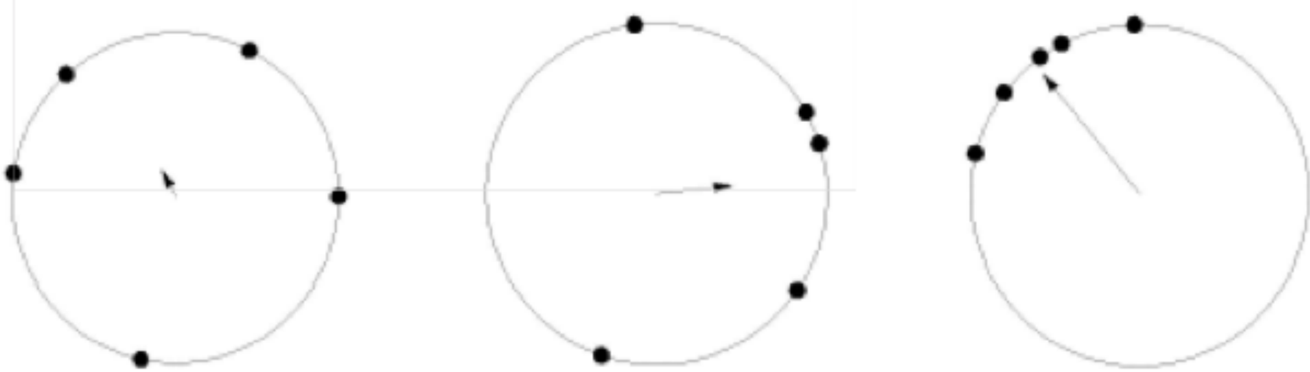
$$re^{i\psi} = \frac{1}{N}\sum_{j=1}^{N} e^{i\theta_j}$$

$$re^{i(\psi-\theta_i)} = \frac{1}{N}\sum_{j=1}^{N} e^{i(\theta_j-\theta_i)}$$

Kuramoto Model

$$r\sin(\psi-\theta_i)=\frac{1}{N}\sum_{j=1}^{N}\sin(\theta_j-\theta_i)$$

$$\frac{d\theta_i}{dt}=\omega_t+K*r*\sin(\psi-\theta_i)$$



(a) $|r| = 0.18$ (b) $|r| = 0.44$ (c) $|r| = 0.91$

Biological Kuramoto Model

$$\frac{d\theta_i}{dt} = \omega_t + \frac{K}{N}\sum_{j=1}^{N}\sin(\theta_j - \theta_i)$$

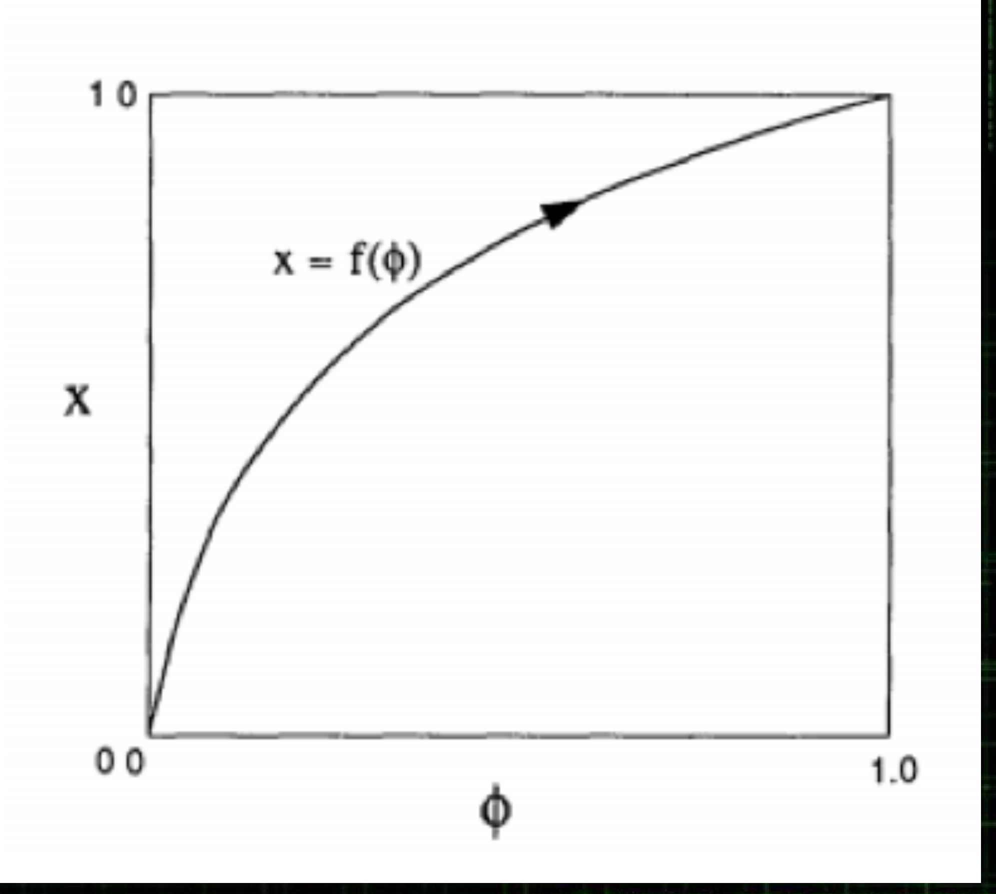
↓

$$\frac{d\theta_i}{dt} = \omega_t + \frac{K}{N}\sum_{j\in\text{fired}}\sin(\theta_j - \theta_i)$$

↑ Perturbation

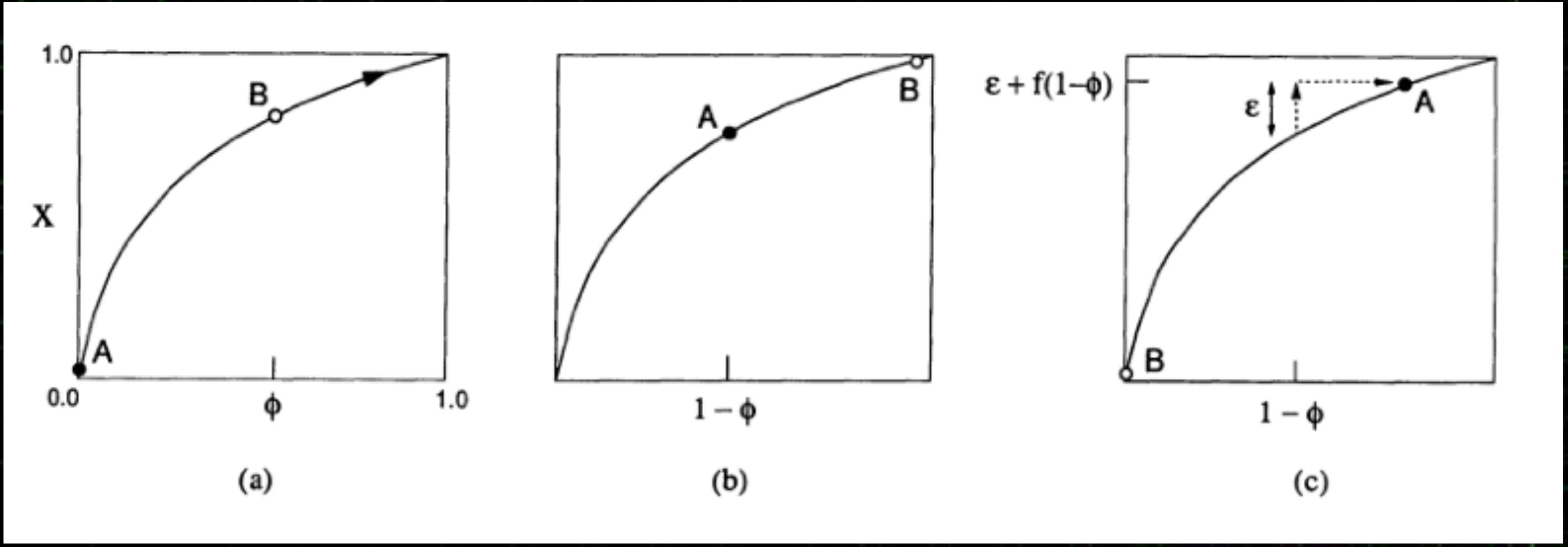
Strogatz Assumptions

- x = f(x)
- f' > 0
- f'' < 0
- g = f^-1
- g' > 0
- g'' > 0



Strogatz Theorem

Any two oscillators that satisfy these conditions always become synchronized.

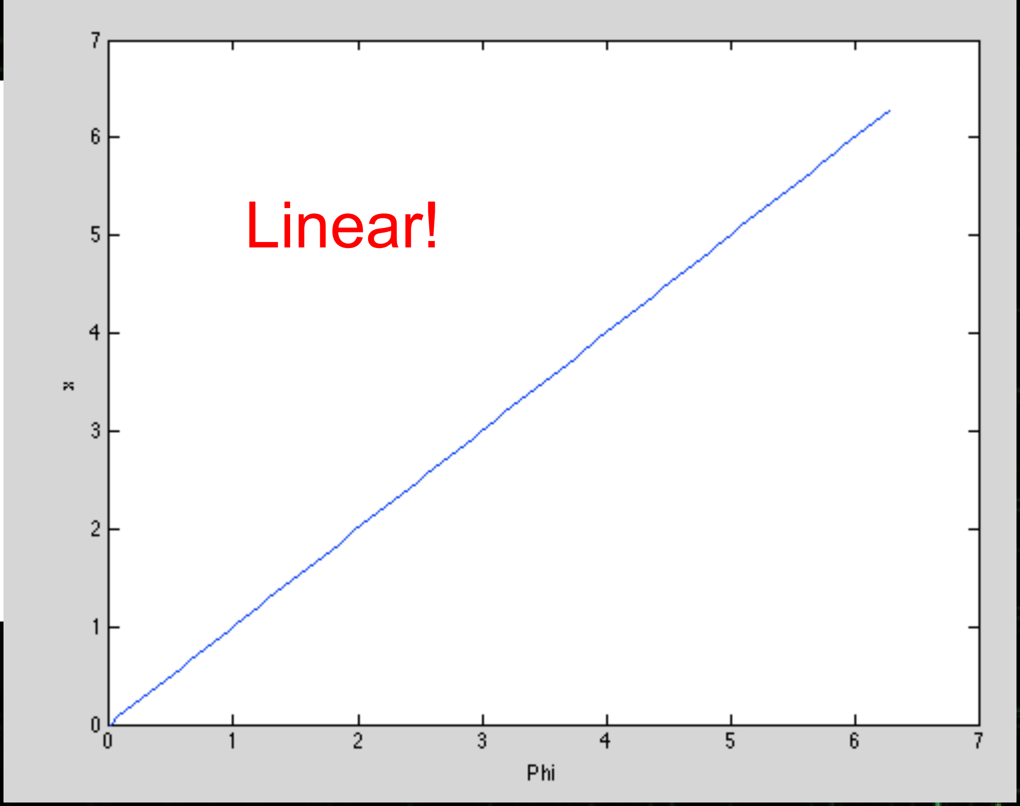


What can we say about the Kuramoto model?

(i) $\phi = \theta$

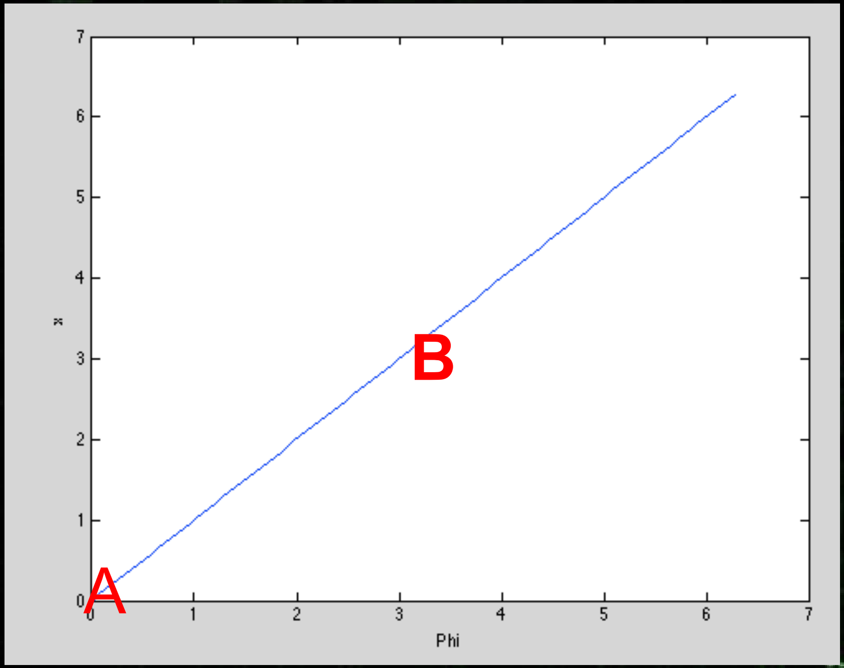
(ii) $\frac{d\theta}{dt} = \omega$

(iii) $f = g = Id \Rightarrow x = \theta$



Return Map

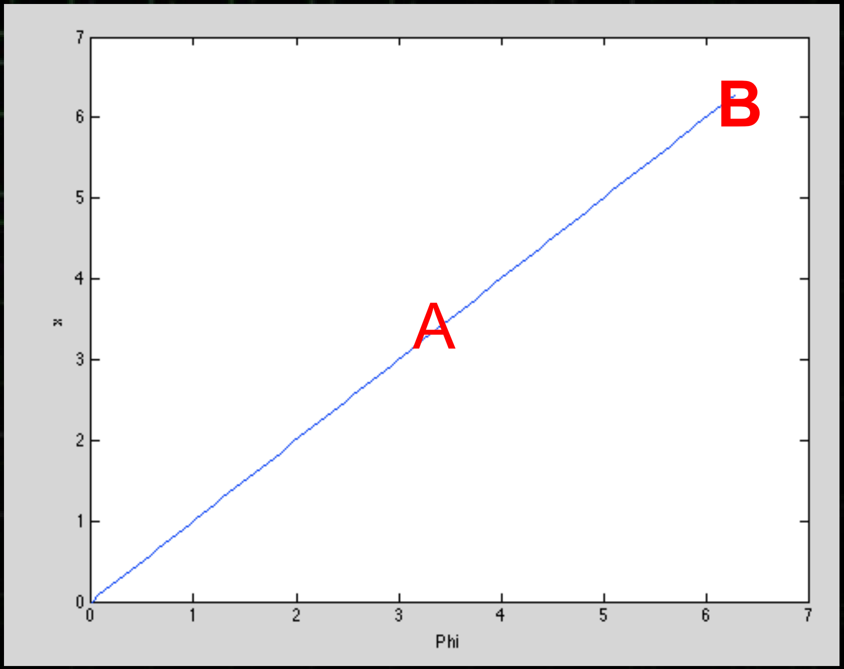
R(θ) maps the phase of B immediately after the next firing of A

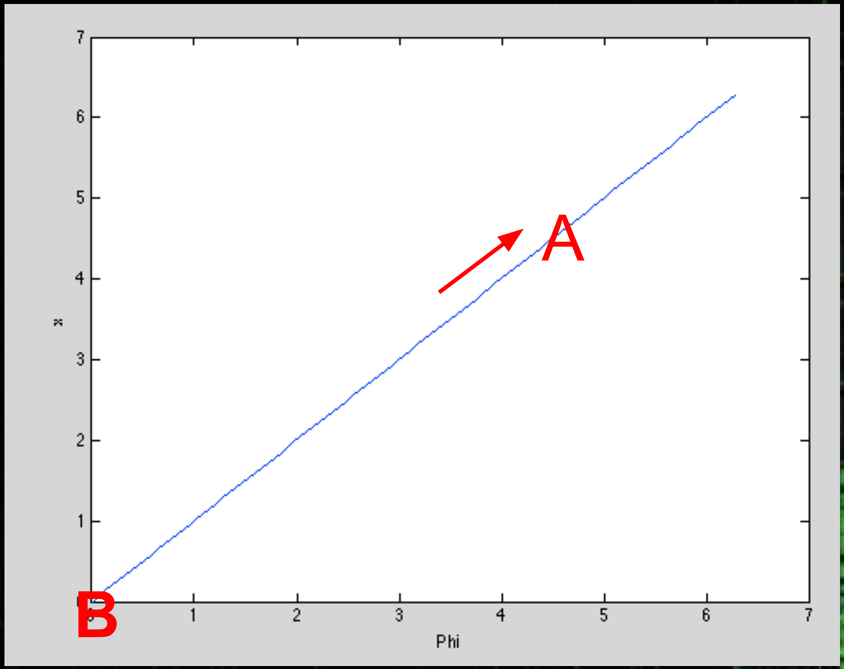


After a time 2π−θ, B fires

A moves to $2\pi - \theta + \sin(\theta)$

Perturbation



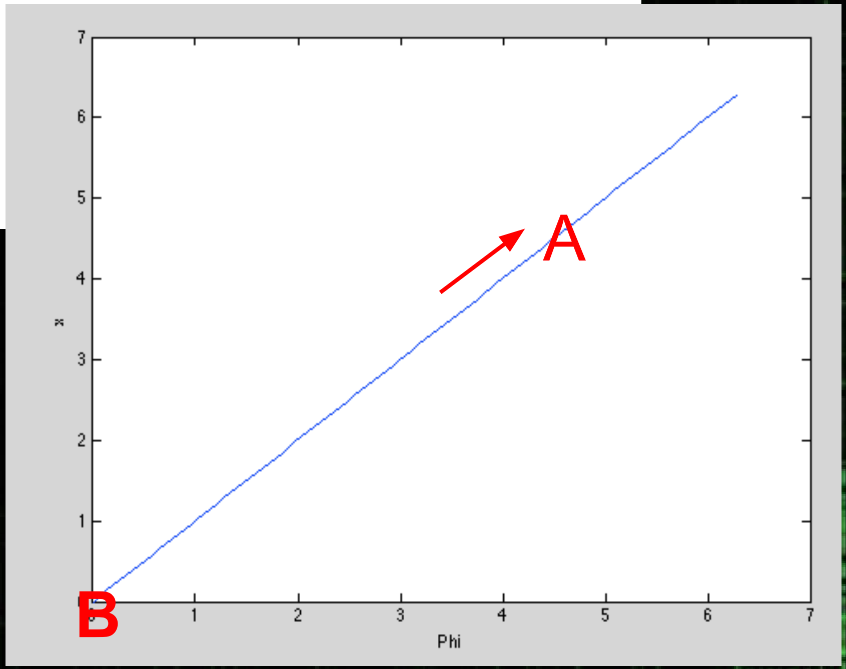


Firing Map

$$h(\theta) = 2\pi - \theta + \sin(\theta)$$

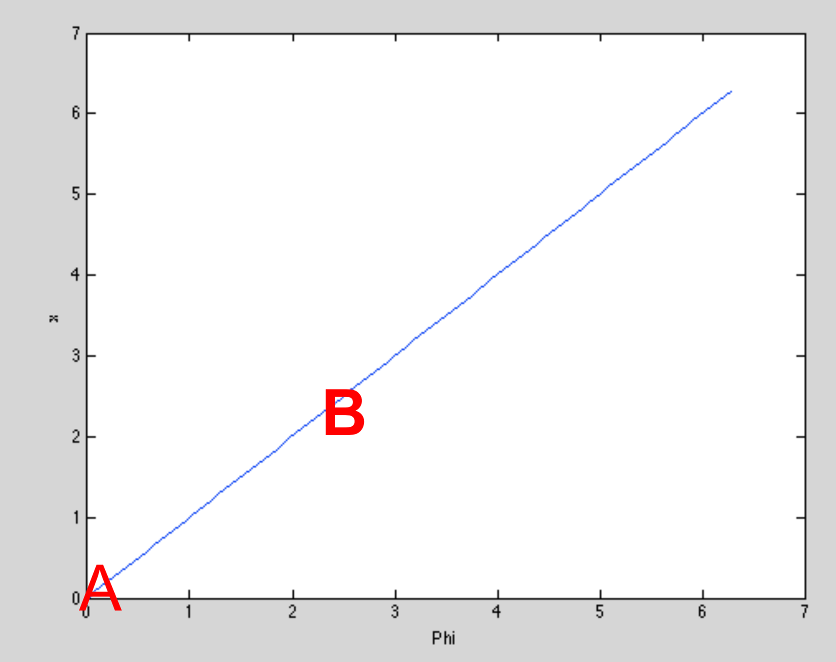
Therefore, the new positions of A and B are:

$$(\theta_A, \theta_B) = (h(\theta), 0)$$



Return Map

After one more iteration:



$$(\theta_A, \theta_B) = (0, h(h(\theta)))$$

And the return map as:

$R(\theta) = h(h(\theta))$, which has fixed points when:

$$h(\theta) = \theta = 2\pi - \theta + \sin(\theta)$$

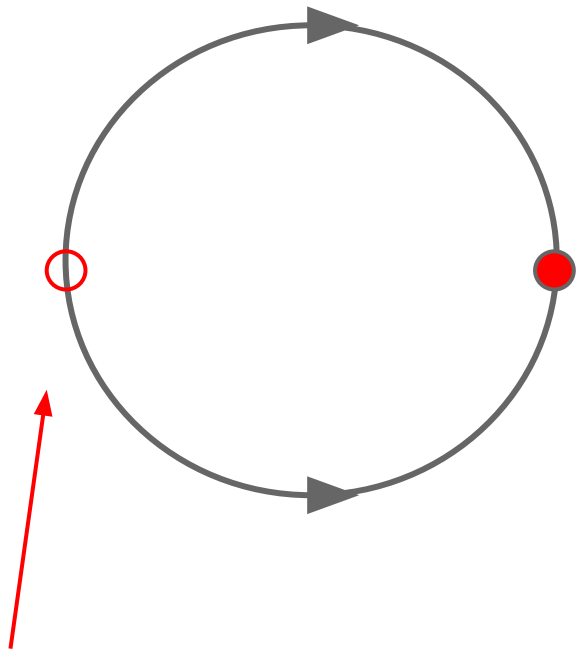
$$\theta^* = 0, \pi$$

Fixed Points

$$R(\theta) = \theta - \sin(\theta) - \sin(\theta - \sin(\theta))$$
$$R'(\theta) = (\cos(\theta) - 1)(\cos(\theta - \sin(\theta)) - 1)$$

Plugging in the fixed points we find:

$$R'(0) = 0 < 1 \text{ (Stable)}$$
$$R'(\pi) = 4 > 1 \text{ (Unstable)}$$



Special Case,

otherwise, Synchronization!

New Perturbation (Kuramoto

$$h(\theta) = 2\pi - \theta + \frac{K}{N}\sin(\theta)$$

New Perturbation (K/N)

And our return map becomes:

$$R(\theta) = -\frac{K}{N}\sin(\theta) - \frac{K}{N}\sin(\theta - \frac{K}{N}\sin(\theta)) + \theta$$

$R(\theta) = \theta$

which has fixed points when:

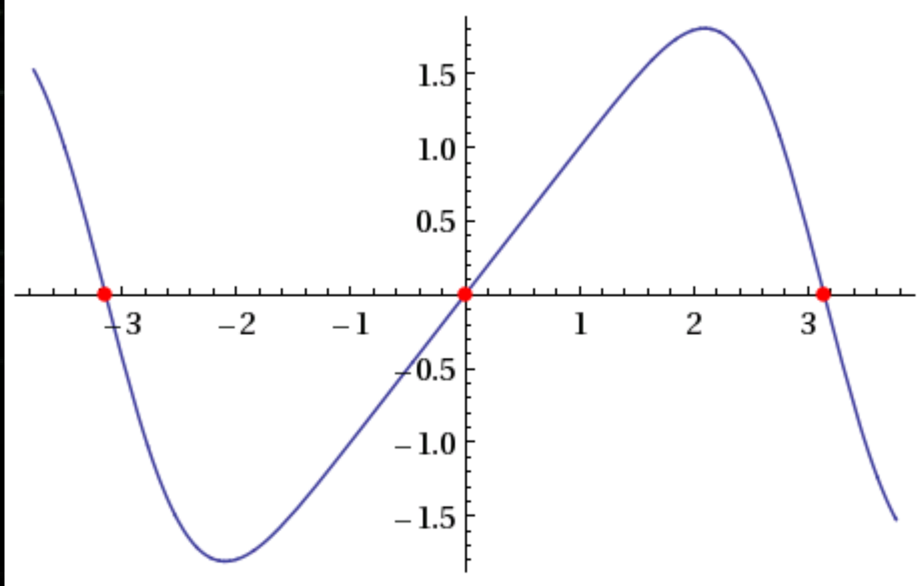
$$\sin(\theta) + \sin(\theta - \frac{K}{N}\sin(\theta)) = 0$$

$$\equiv \sin\theta = \frac{2N\theta}{K}$$

Fixed Points

$$\equiv \sin\theta = \frac{2N\theta}{K}$$

which has fixed points $n\pi$ for $\frac{K}{N} \geq 0$,



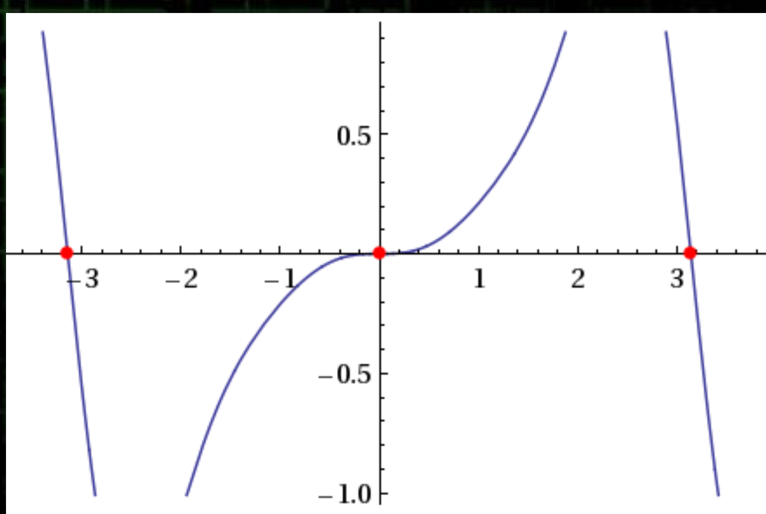
R(θ) = θ, K/N = 1

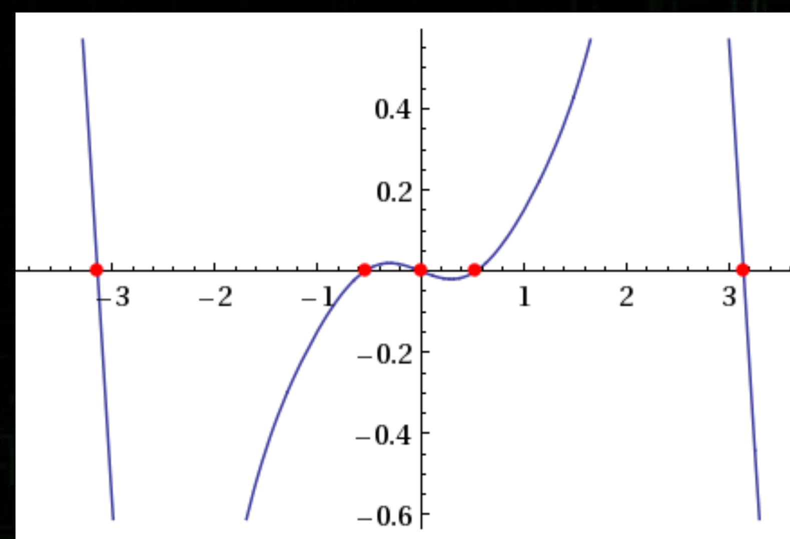
Supercritical Pitchfork Bifurcation

bifurcation when $\dfrac{K}{N} = 2$, since:

$$R'(0) = (\frac{K}{N} - 1)^2 > 1 \text{ when } \frac{K}{N} > 2$$

and the two new fixed points have $R' < 1$



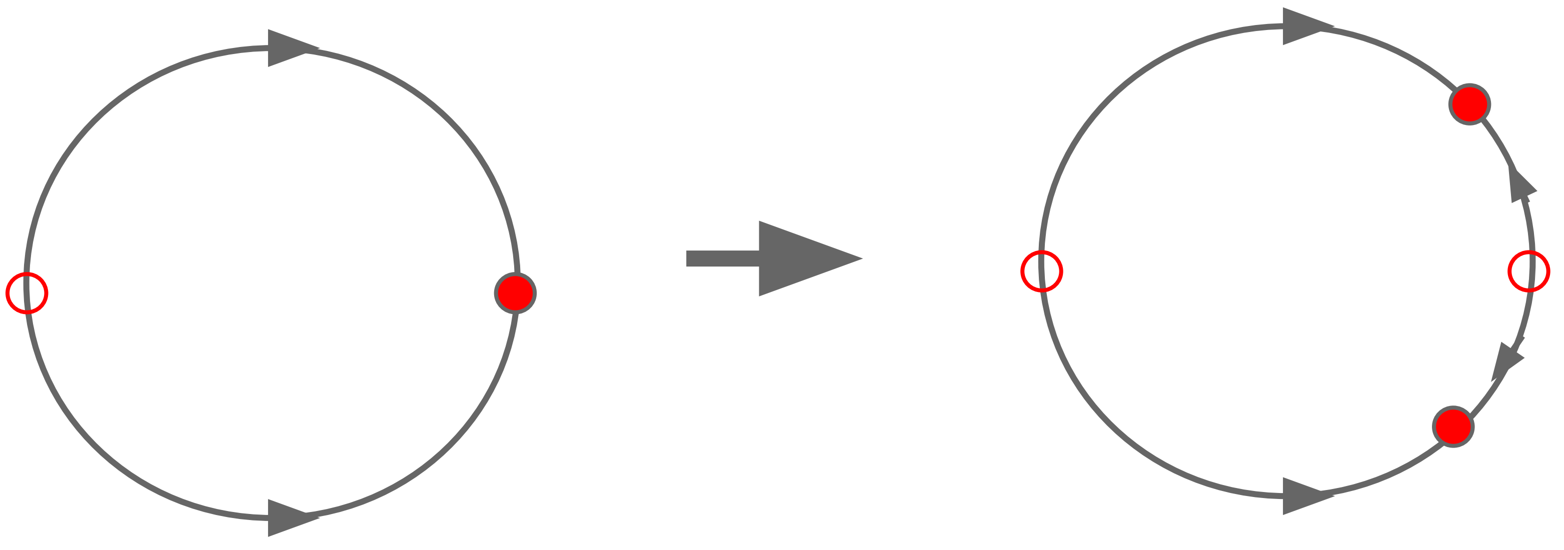


K/N = 2

$R(\theta) = \theta$

K/N = 2.1

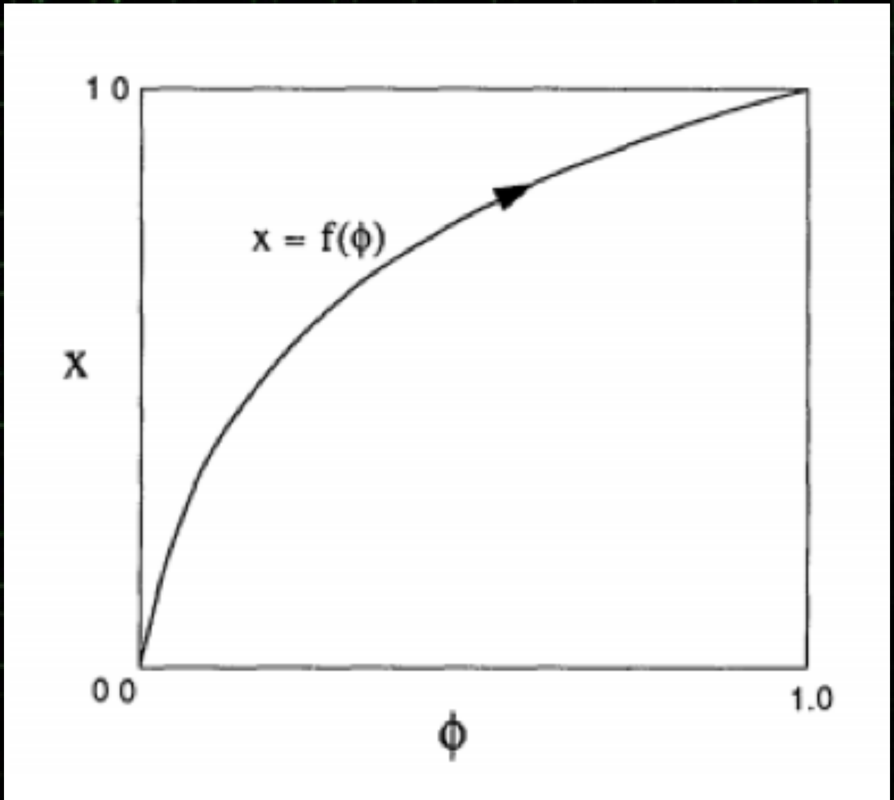
Supercritical Pitchfork Bifurcation

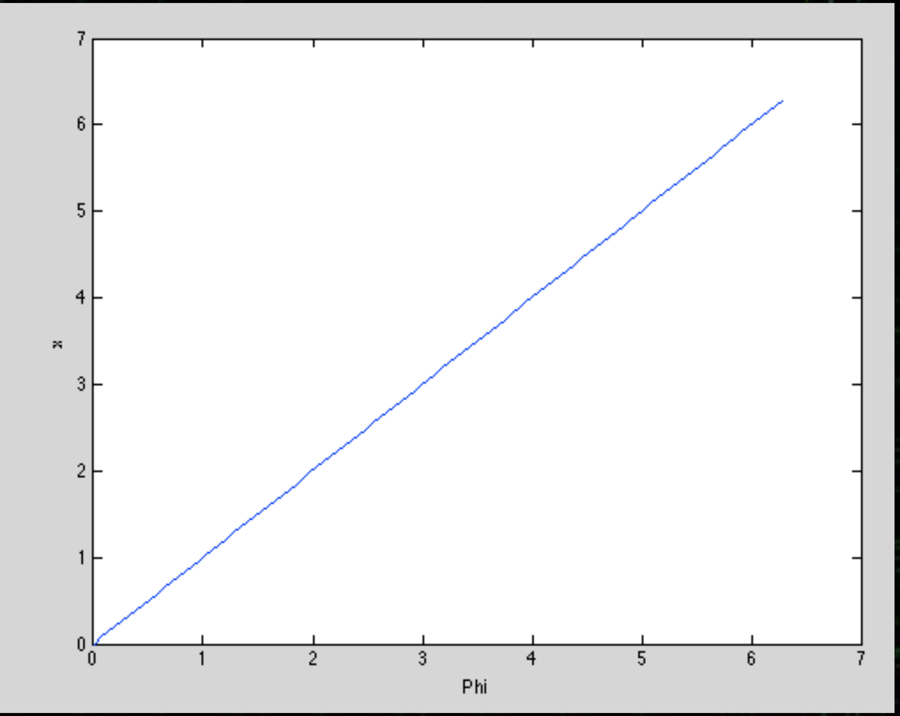


K <= 2N, Synchronization

K > 2N, Entrainment

Strogatz vs Kuramoto





-f' need not be concave down
-perturbation can be periodic

The Hypothesis

- As the fireflies are connected to more neighbors the time for synchronization decreases
- There is an optimal coupling constant that minimizes the time for synchrony

Variables

- Independent
  - Number of connections
  - Coupling strength (K in the Kuramoto Model)
- Dependent
  - The time until synchronization

Experimental Assumptions

- The distribution of initial conditions is random
  - Each set of independent variables was examined over an ensemble of fifteen sets of random initial conditions
- Each firefly evolves in time according to the same dynamical law
  - Biologically, a given species has the same instinct for flash stimulation
  - Mathematically, dynamical equation, flash threshold, and intrinsic frequency are all the same

What are we trying to measure?

$$\tau = F(\phi, c, K)$$

$$\phi \equiv phase\ distribution$$

$$c \equiv quantity\ of\ connections$$

$$K \equiv coupling\ strength$$

Our Experimental Model

$$\frac{d\theta_i}{dt} = \omega_t + \frac{K}{N} \sum_{j \in fired} A_{i,j} sin(\theta_j - \theta_i)$$

Addition of Coupling Matrix

Radial Line of Sight

$$\frac{d\theta_i}{dt} = \omega_t + \frac{K}{N} \sum_{j \in fired} A_{i,j} sin(\theta_j - \theta_i)$$

Symmetric

- 1 <= i, j <= 48
- If fireflies i and j are within visual range of each other, then A(i,j)=A(j,i)=1,
- if not, then A(i,j)=A(j,i)=0.
  - A(i,i)=0 for all i

Experimental Cases

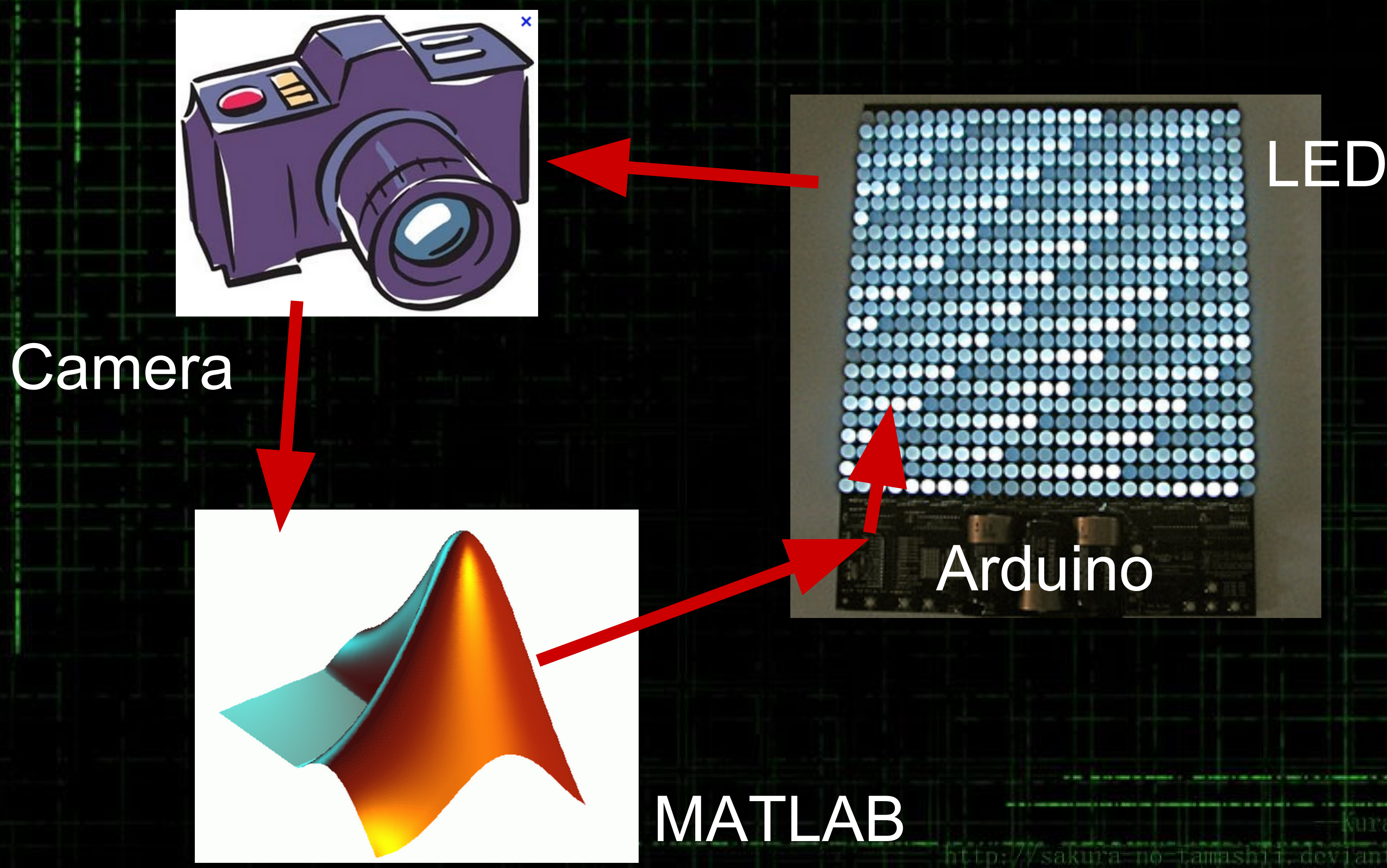
Matrix, A

1. R = 1, c = 4
2. R = 2, c = 8
3. R = sqrt(5), c = 12
4. R = 3, c = 20
5. R = sqrt(13), c = 27
6. R = 4, c = 33
7. R = sqrt(20), c = 40
8. R = 5, c = 46
9. R = 6, c = 47

Coupling Strengths

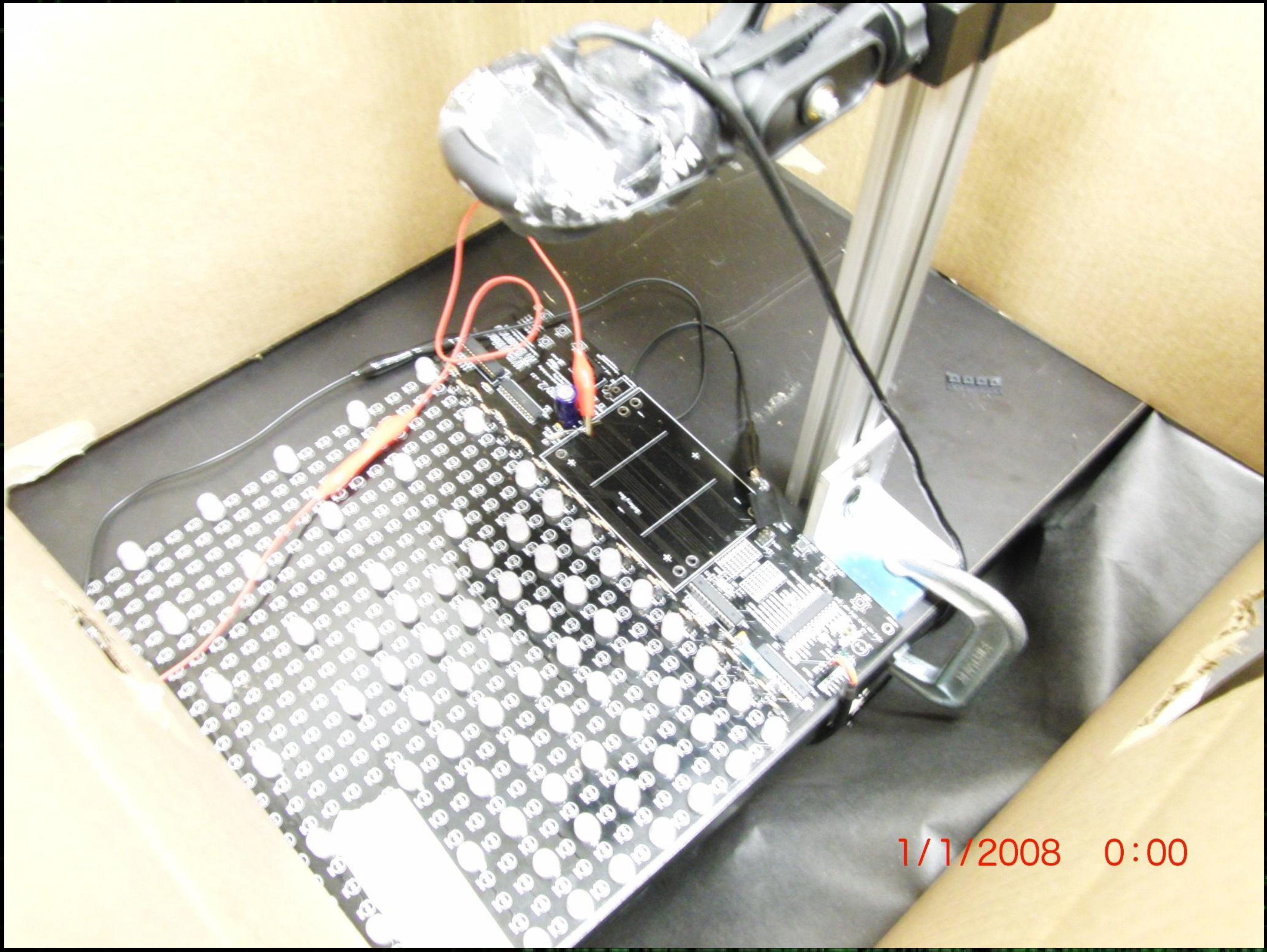
1. K = 1
2. K = 2
3. K = 5
4. K = 7
5. K = 10
6. K = 15
7. K = 20
8. K = 25
9. K = 30

Experimental Schematic



Experimental Design

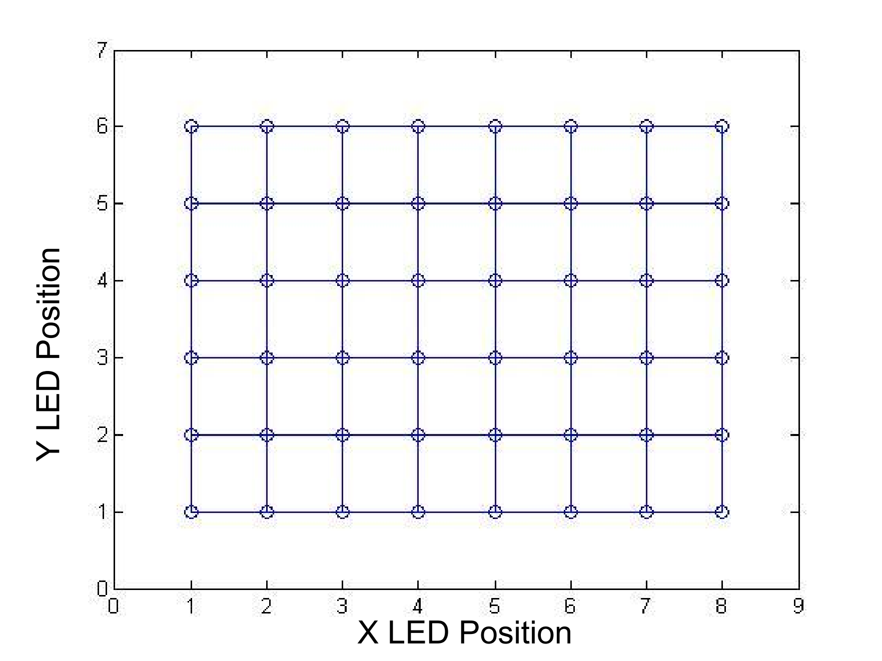
Experimental Design



Line of Sight Adjacency Matrix

- Points within circle are connected
- Most models assume global coupling but fireflies do not have infinite vision
- Approximation for physical boundaries in a forest

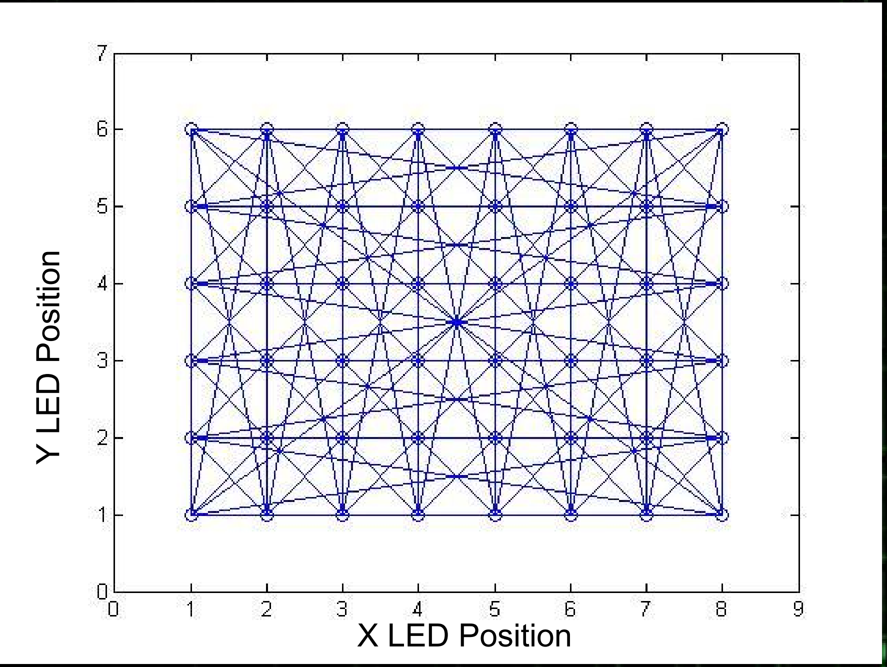
Radius = 1



Line of Sight Adjacency Matrix

- Points within circle are connected
- Most models assume global coupling but fireflies do not have infinite vision
- Approximation for physical boundaries in a forest

Radius = 2



Line of Sight Adjacency Matrix

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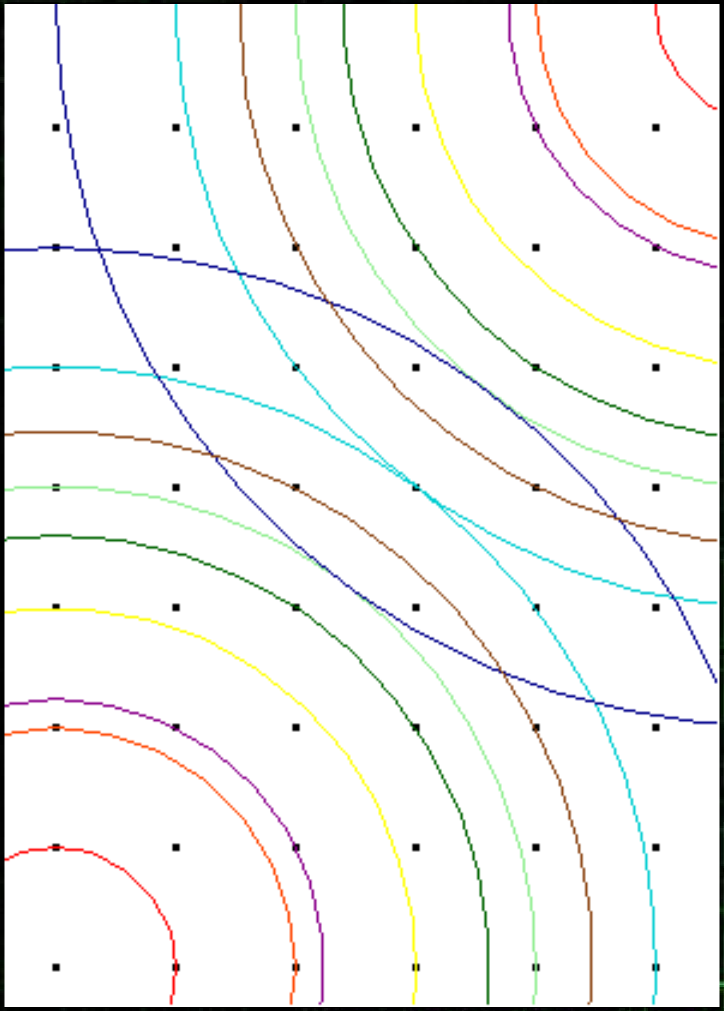
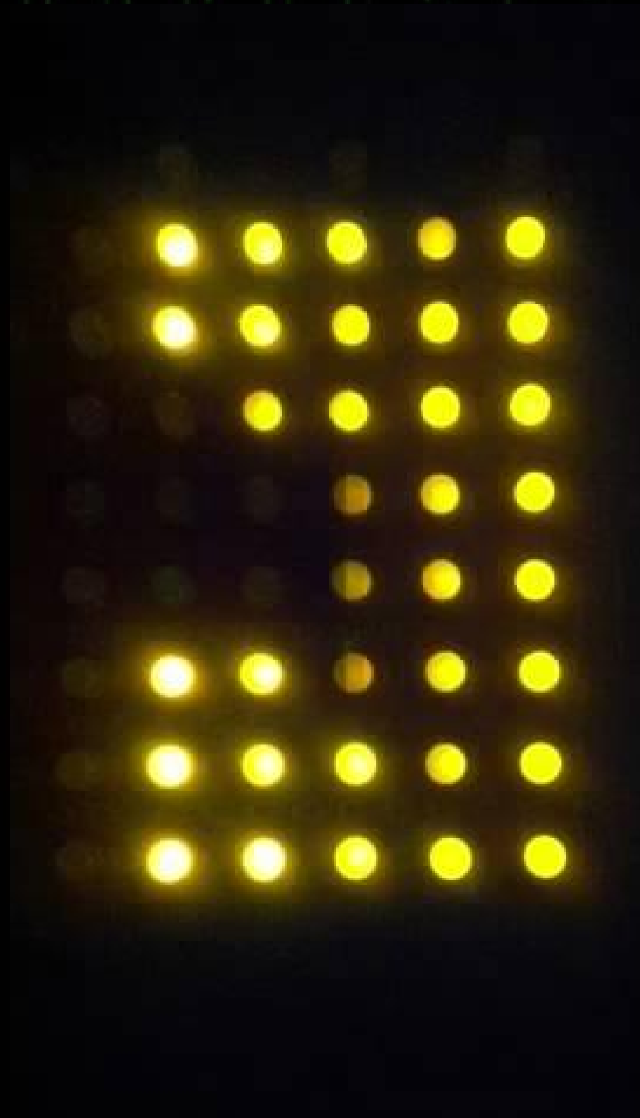
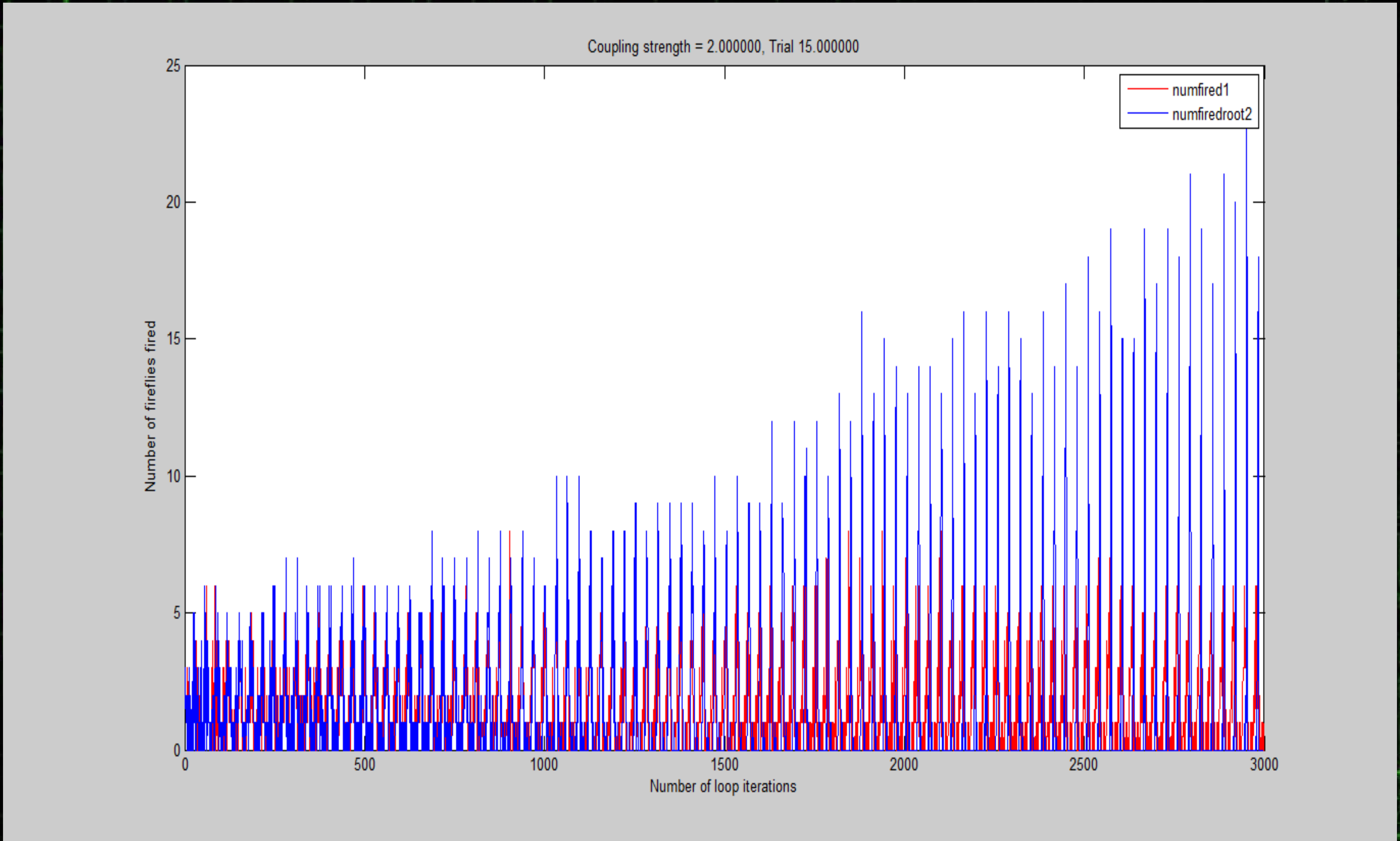


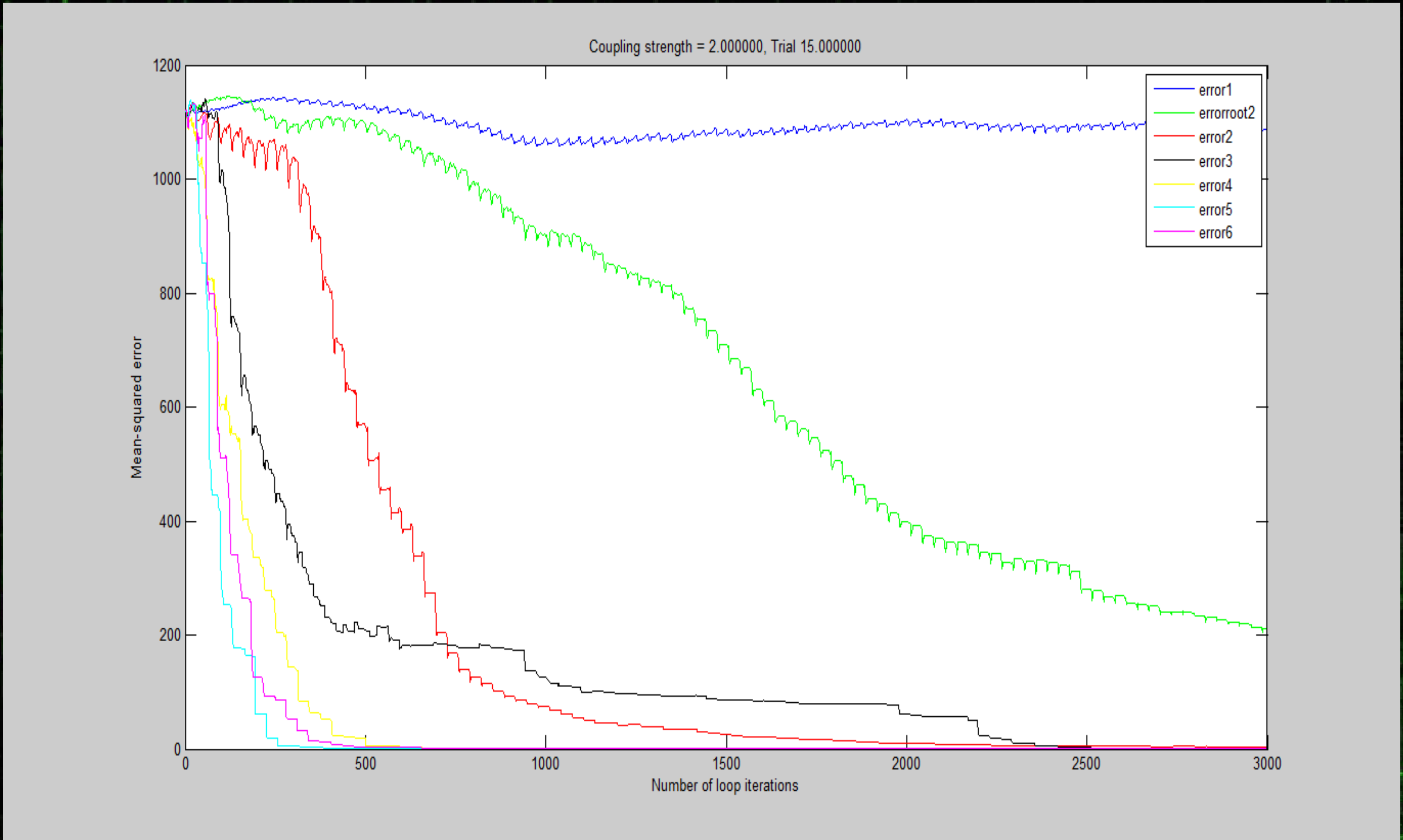
Example Experiment Trial



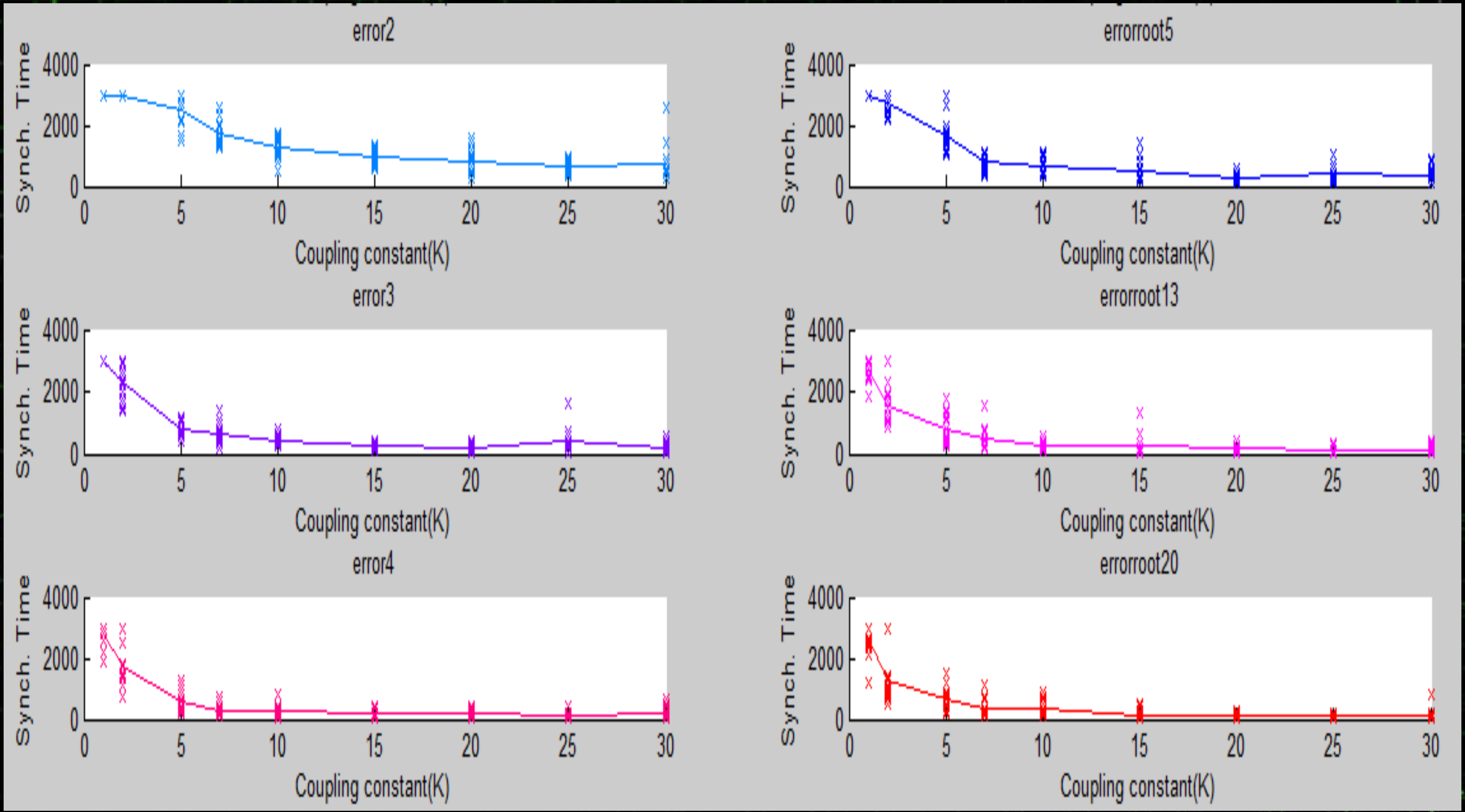
Experimental Data



Experimental Data

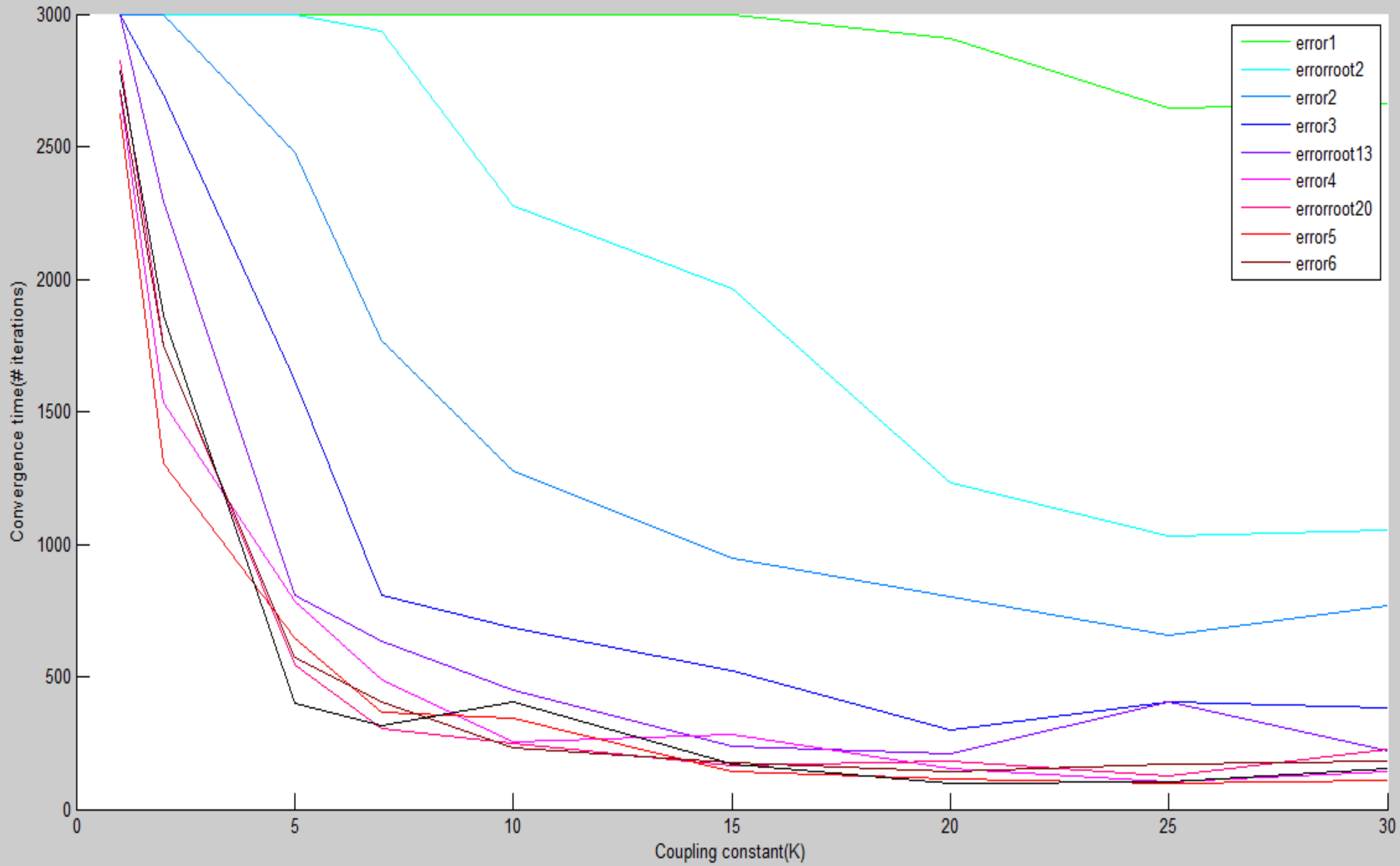


Experimental Data

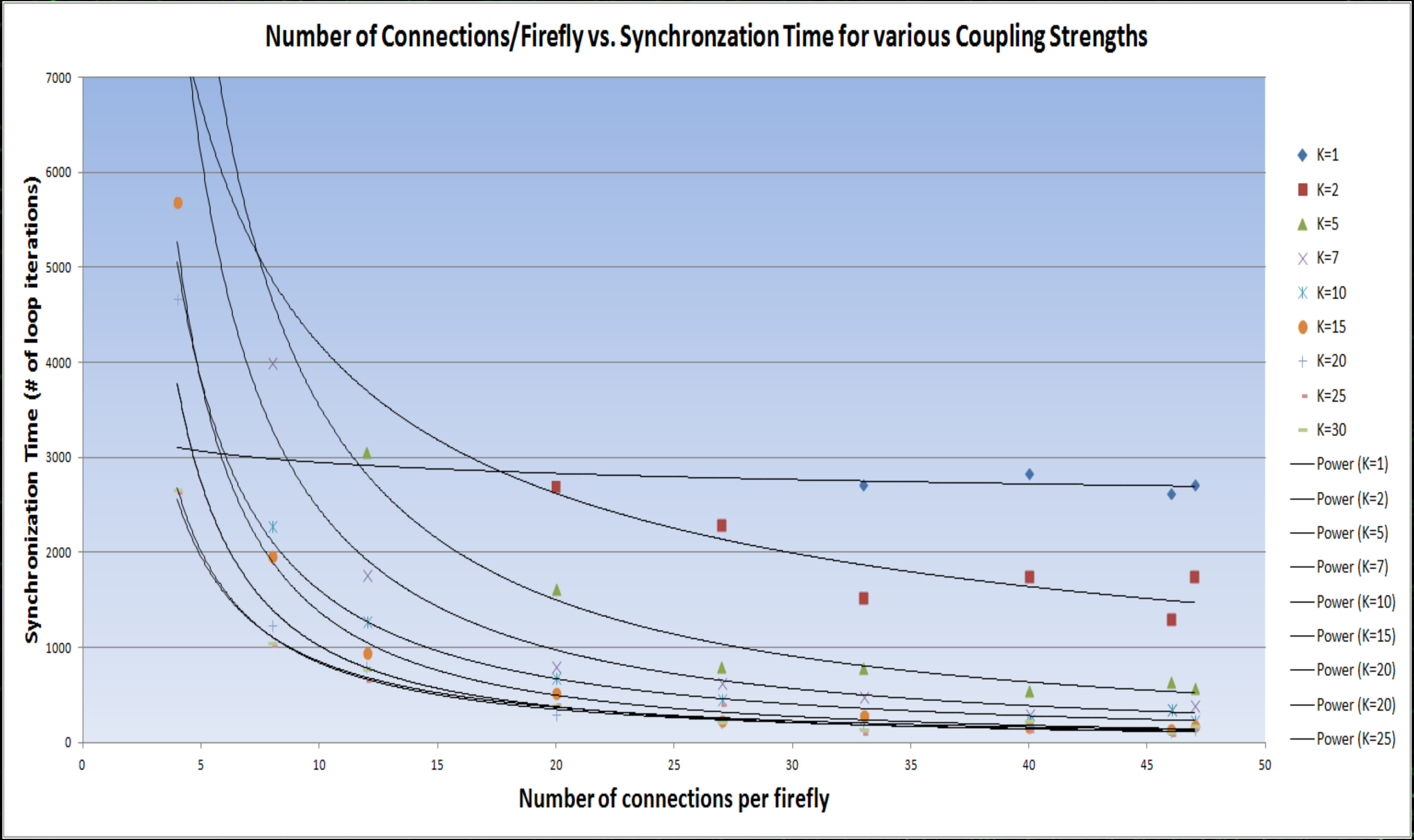


15 Trials, Average

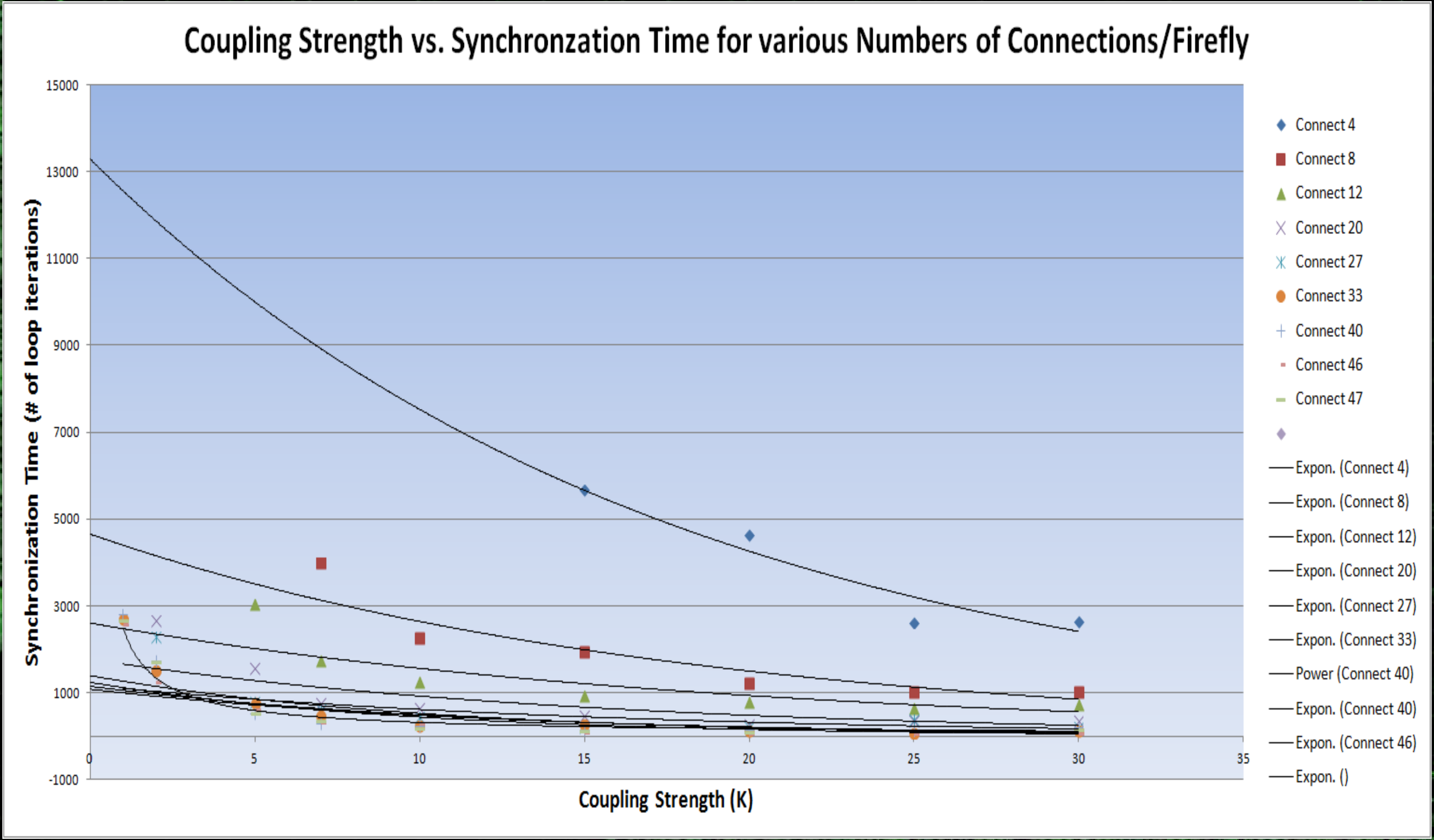
Experimental Data



Experimental Data



Experimental Data



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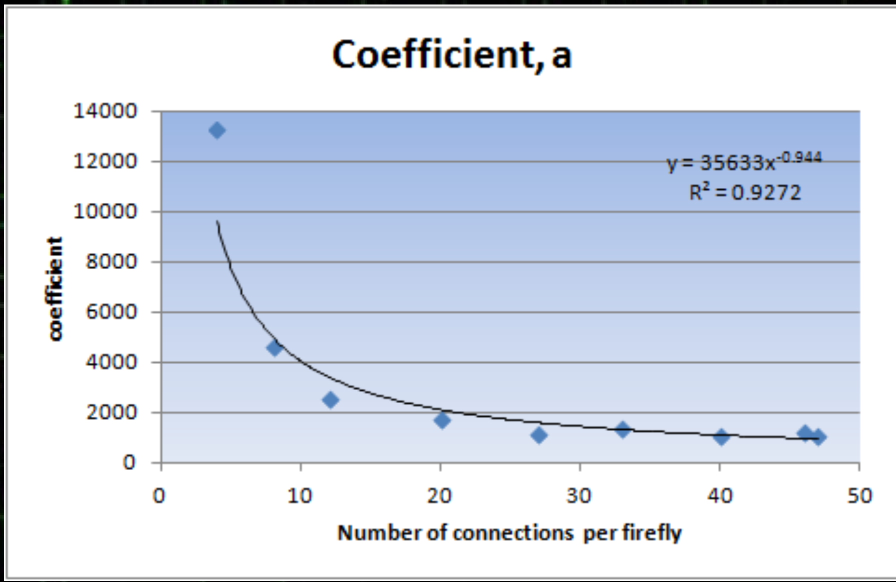
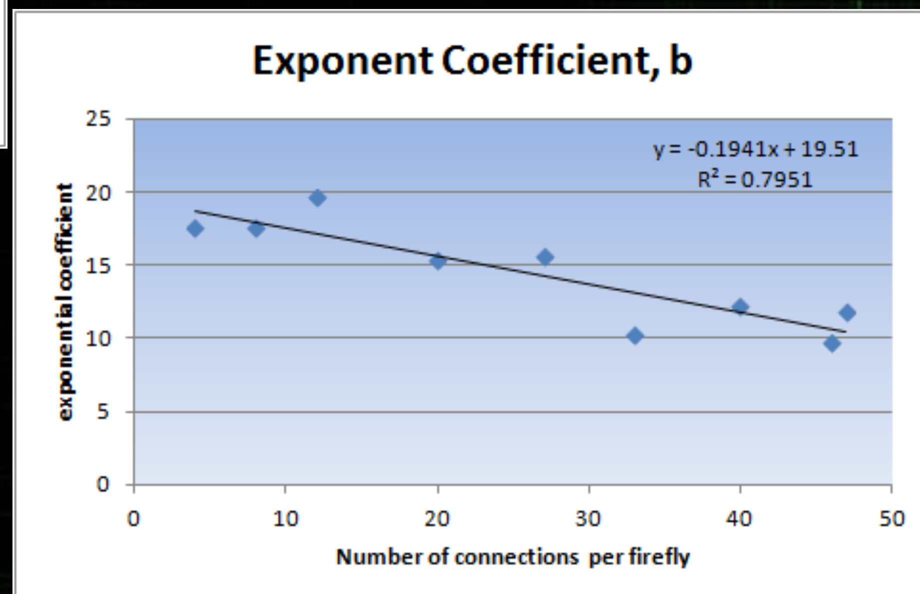


Fitted to the form:

$$\tau = ae^{bK}$$



To achieve:

$$\tau = \frac{35600}{c^{-0.94}} e^{\frac{-K}{(20-0.19c)}}$$

Analysis

- The synchronization time, τ, is dependent on the coupling constant and the number of connected fireflies
- From fitting parameters a coarse equation can be established

$$\tau = \frac{35600}{c^{-0.94}} e^{\frac{-K}{(20-0.19c)}}$$

Sources of Error

- Some of the higher connection matrices are asymmetric from an error
- The model incorporates an additional low order perturbation when updating the other fireflies

Conclusion

- Appears to be a quantifiable relation between the convergence time for a population of our model's fireflies and their numbers of connections and coupling strength, even with the simplifying assumption that initial phase effects can be reduced by taking averages across "large" sample sizes.

Suggestions for Future Work

- How would...
  - a larger N
  - a smaller K
  - asymmetric coupling
  - non-identical fireflies

  ...affect the dynamics?

  Will dynamic removal or addition of connections result in symmetry breaking?

  Are there better biological models for fireflies, and do they result in synchrony?

Acknowledgements

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Questions?