Biological Synchronization

First example of spontaneous synchronization

- Huygens, 1665
- Inventor of pendulum clocks
- Hang two clocks to the same wall
- In half an hour they always regained synchrony
- Opposite wall: one loosing 5 sec a day relative to the other
- *Theory of coupled oscillators*

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Published online 21 February 2002 | Nature | doi:10.1038/news020218-16

News

Synchronized swinging

Ancient pendulum conundrum solved.

John Whitfield

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Twin pendulums mirror each other's movements.

US physicists have solved a 350-year-old riddle of why the pendulums of two clocks become synchronized. The clocks were the first example of spontaneous synchronization, a phenomenon found throughout nature from cells to the Solar System.

In 1665, the Dutch physicist Christiaan Huygens, who patented the pendulum clock, was working on a way to calculate longitude on board ships. His approach was to put two clocks in a single housing, so that if one broke down, the other could provide a back-up.

Ill in bed, with nothing better to do than watch his clocks, Huygens noticed that no matter where they started, within about half an hour the two pendulums swung towards and away from each other in unison. His observations - made 20 years before Newton devised the laws of mechanics - have gone unexplained until now.

Physicist Michael Schatz and his colleagues at the Georgia Institute of Technology reconstructed Huygens' two-in-one clock box from his lab notes and diagrams.

They found that the clocks' behaviour resulted from the 40 kg of lead ballast in the apparatus, intended to hold the clocks fast at sea.

SCIENTIFIC REPORTS

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Huygens synchronization of two clocks

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Received: 30 January 2015
Accepted: 12 May 2015
Published: 23 July 2015

The synchronization of two pendulum clocks hanging from a wall was first observed by Huygens during the XVII century. This type of synchronization is observed in other areas, and is fundamentally different from the problem of two clocks hanging from a moveable base. We present a model explaining the phase opposition synchronization of two pendulum clocks in those conditions. The predicted behaviour is observed experimentally, validating the model.

Andronov model

Not so obvious: https://www.youtube.com/watch?v=SGgbRkix_hY

First explanation

- Huygens wrote about "sympathy of two clocks" in a letter to his father
- He also provided a qualitative explanation of this effect of *mutual synchronization*;
- he correctly understood that the conformity of the rhythms of two clocks had been caused by an *imperceptible motion of the beam*.

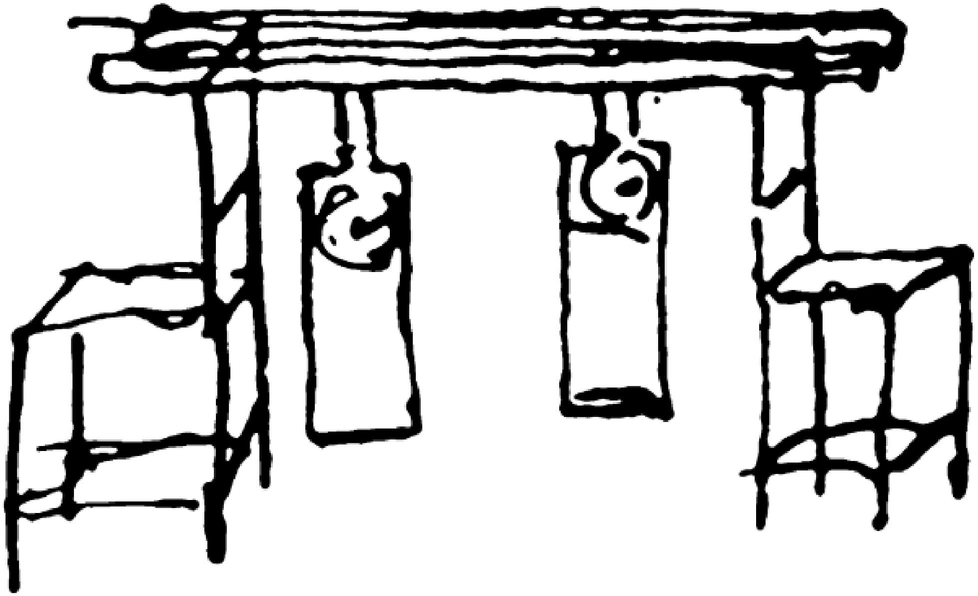

Figure 1.2. Original drawing of Christiaan Huygens illustrating his experiments with two pendulum clocks placed on a common support.

Oscillating metronomes – a demonstration

https://www.youtube.com/watch?v=bl2aYFv_978

- The burst into spontaneous applause
- Human physiology: walking, breathing
- Neuron network
- Pacemaker cells in the heart
- Chirping of crickets
- Fireflies
- Etc.

https://www.youtube.com/watch?v=ZGvtnE1Wy6U

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First models of biological oscillators

- Arthur Winfree, late 1960s
  - Ignored *all* biological differences and focused on the only common things: the ability to *send* and *receive signals*
  - Complication: both of these are often a function of phase
    - “Influence function” – what signal it sends
    - “Sensitivity function” – how an oscillator responds to the signals it receives
    - ➢Oscillators can advance or delay, depending on where they are in their cycle when they receive a pulse. (Experiments show that most biological oscillators are like this)
  - ❖Assumptions:
    - ❖All the oscillators in a given population have the same influence and sensitivity function
    - ❖But the natural frequencies can vary, according to a bell shape
    - ❖Connectivity (the way the oscillators are connected)

Kuramoto model

- 1975
- assumptions:
  - – the oscillators are identical or nearly identical (bell-shaped distribution of natural frequencies)
  - – the interactions depend sinusoidally on the phase difference between each pair of objects.

- Later it has found widespread applications in other fields too (neuroscience, physical systems, etc.)

The Kuramoto model (KM)

- Continuous time and phase
- Consists of a population of *N* coupled oscillators
- Each tries to run independently at its own frequency, while the coupling tends to synchronize it to all the others
    - ϕ_i : the phase of oscillator *i* (in the sense of mod 2π)
    - t : time
    - T_i : periodic time
    - $\nu_i = \frac{1}{T_i}$: natural frequency
    - $\omega_i = \frac{2\pi}{T_i}$: natural angular frequency
- One oscillator (an oscillator without interaction):

$$\frac{d\phi}{dt} = \omega$$

The Kuramoto model in mean field approximation

- IN GENERAL: *N* coupled oscillators interacting with each others pairwise :

$$\frac{d\phi_i}{dt} = \omega_i + \sum_{j=0}^{N-1} \Gamma_{ij}(\phi_j - \phi_i)\,, \qquad\qquad (i,j = 0,1,\dots,N-1)$$

- $\Gamma_{ij}(\Delta\phi)$: interaction, a function with 2π periodicity
- All the oscillators interact with each other the same way (this was the simplifying assumption of Kuramoto):

$$\Gamma_{ij}(\phi) = \frac{K}{N}\sin(\phi)\,, \qquad\qquad (i,j = 0,1,\dots,N-1)$$

- K : strength of the coupling
- If $\mathrm{K} > 0$ → Γ minimizes the phase difference

The Kuramoto model in mean field approximation

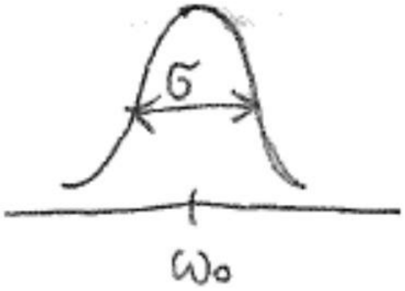
- The basic formula of the KM with MF approximation:

$$\boxed{\frac{d\phi_i}{dt} = \omega_i + \frac{K}{N}\sum_{j=0}^{N-1}\sin(\phi_j - \phi_i)}, \qquad (i, j = 0,1,\dots,N-1)$$

- How do such oscillators synchronize?
- The interplay between the coupling strength and the distribution of the natural frequencies determines how many oscillators are synchronized.
- How can we measure the level of synchronization?
  - Order parameter: An order parameter is a measure of the degree of order across the boundaries in a phase transition system; it normally ranges between zero in one phase and nonzero in the other.
- A trivial order parameter can be: $R = \frac{N_S}{N}$, where N_s is the number of synchronized units

Order parameter for the Kuramoto model

- The “Kuramoto order parameter” is more appropriate to monitor the transition towards synchronization)
- Let us assume that
  - the ω_i natural frequencies are taken from a Gaussian distribution $g(\omega)$
  - The expected value of the $g(\omega)$ density function is ω_0, with σ standard deviation



$$g(\omega) = \frac{1}{N}\sum_{i=0}^{N-1} \delta(\omega_i - \omega) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(\omega-\omega_0)^2}{2\sigma^2}}$$

Defining the order parameter

- Parameter transformation:

$$\Psi_i \coloneqq \phi_i - \omega_0 t$$

$$\omega_i \leftarrow \omega_i - \omega_0$$

(ω_0 : average natural frequency)

- The Kuramoto formula is invariant to the above transformation:

$$\frac{d\psi_i}{dt} = \omega_i + \frac{K}{N}\sum_{j=0}^{N-1} \sin(\psi_j - \psi_i) \ ,(i,j = 0,1,\dots,N-1)$$

- $\theta(t)$: the vectorial average of the (transformed) ψ_i unit vectors
- Now we can define the order parameter as next (as the *complex mean field* of the population):

$$z(t) \coloneqq Z(t)e^{i\theta(t)} = \frac{1}{N}\sum_{j=0}^{N-1} e^{i\psi_j(t)}$$

(here i is not the index of an oscillator, but $\sqrt{-1}$)

Defining the order parameter – cont.

$$\underbrace{z(t)}_{\text{Complex order param.}} := \underbrace{Z(t)}_{\text{Real part}} e^{i\theta(t)} = \frac{1}{N}\sum_{j=0}^{N-1} e^{i\psi_j(t)}$$

$$\underbrace{\frac{1}{N}N}_{=1}\left|e^{i\psi_j(t)}\right|$$

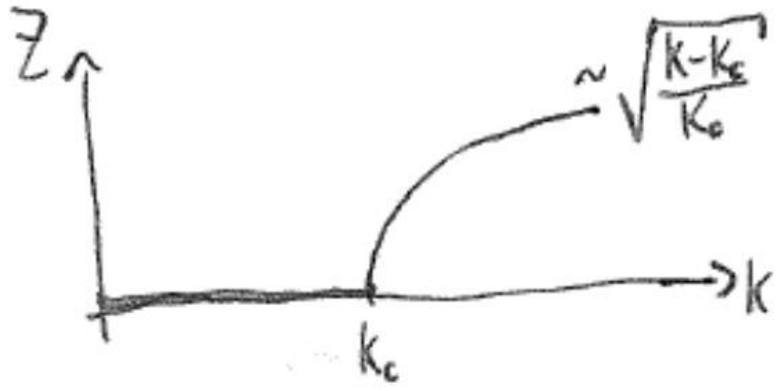
- real part of $z(t)$, → $Z = |z|$
- the *order parameter* has the following properties:
  - Expresses the “closeness” of the ψ_i unitvectors
  - If $Z \approx 1$ → the ψ_i phases are close to each other
  - If $Z \approx 0$ → the ψ_i phases point in random direction

Bifurcation

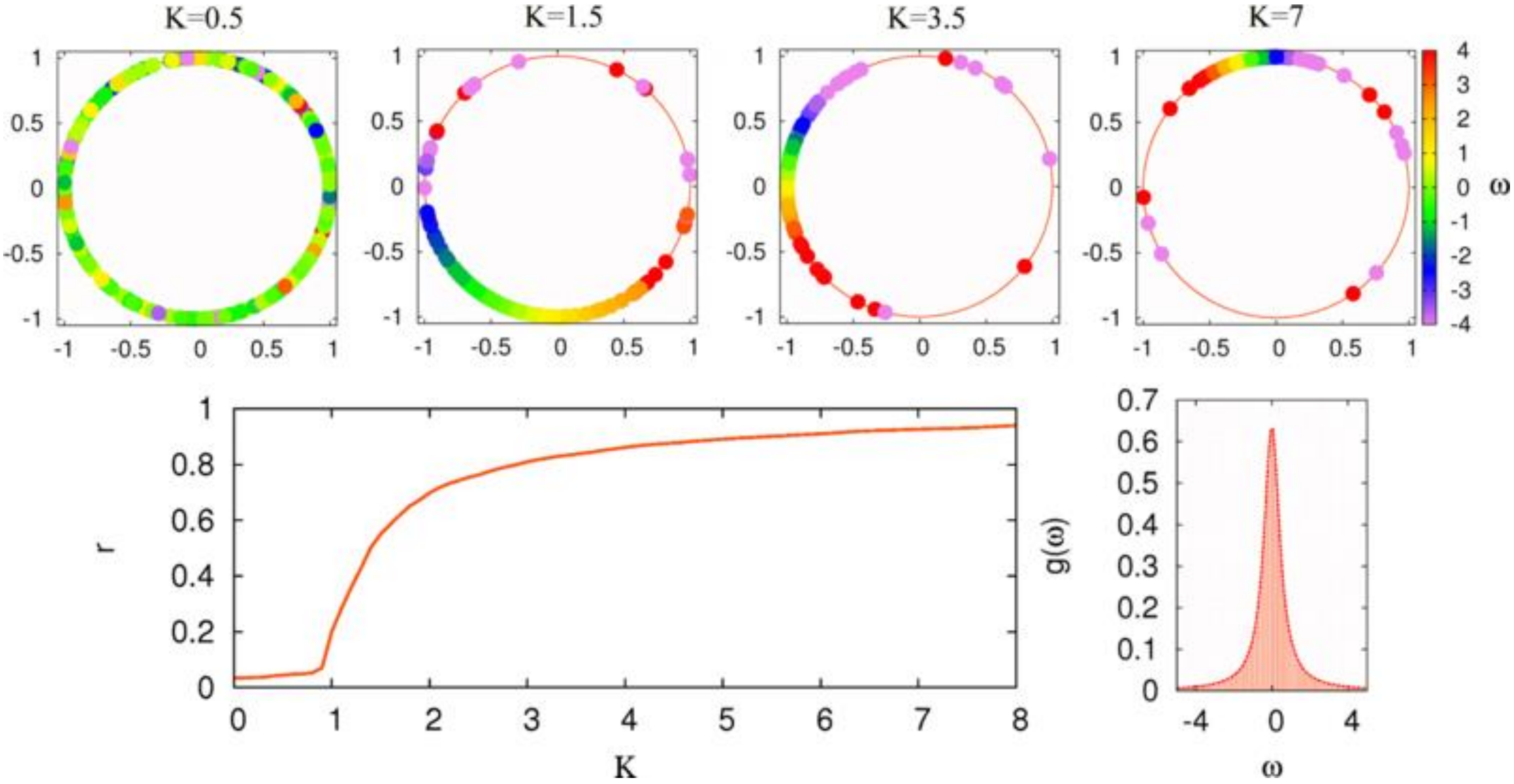
- In the uncoupled limit (*K*=0) each element i describes limit-cycle oscillations with characteristic frequency ω_i.
- Kuramoto showed that, by increasing the coupling *K* the system experiences a transition towards complete synchronization, i.e. , a dynamical state in which $\psi_i(t) = \psi_j(t)$ for $\forall i, j$ and $\forall t$.
- This transition shows up when the coupling strength exceeds a critical value whose exact value is

$$K_C = \frac{2}{\pi \cdot g(\omega_0)}$$

(ω_0 is the mean frequency of the $g(\omega)$ frequency distribution)



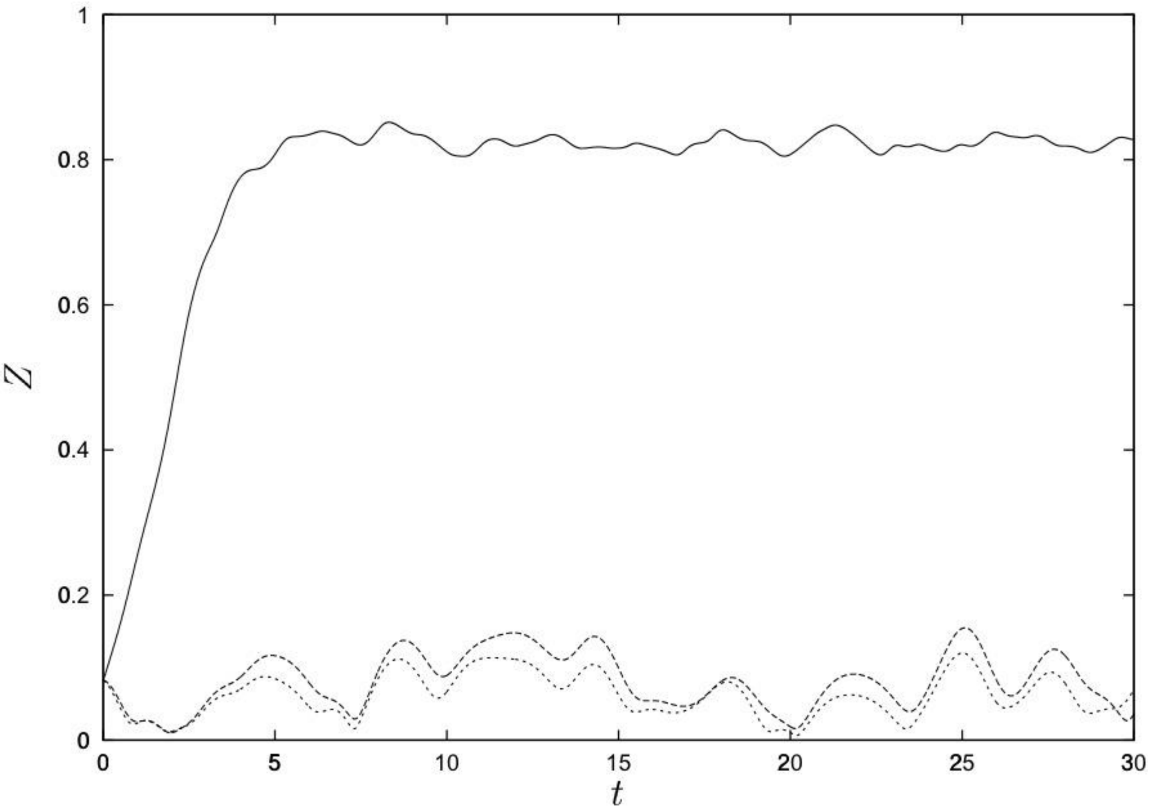
From: Mendoza et al., 2014, Synchronization in a semiclassical Kuramoto model.



Synchronization in the classical Kuramoto model. Each panel on the top shows the collection of oscillators situated in the unit circle (when each oscillator *j* is represented as $e^{i\psi_j(t)}$).
The color of each oscillator represents its natural frequency. From left to right we observe how oscillators start to concentrate as the coupling *K* increases. In the panels below we show the synchronization diagram, i.e. , the Kuramoto order parameter *Z* as a function of *K* . It is clear that $K_c = 1$.

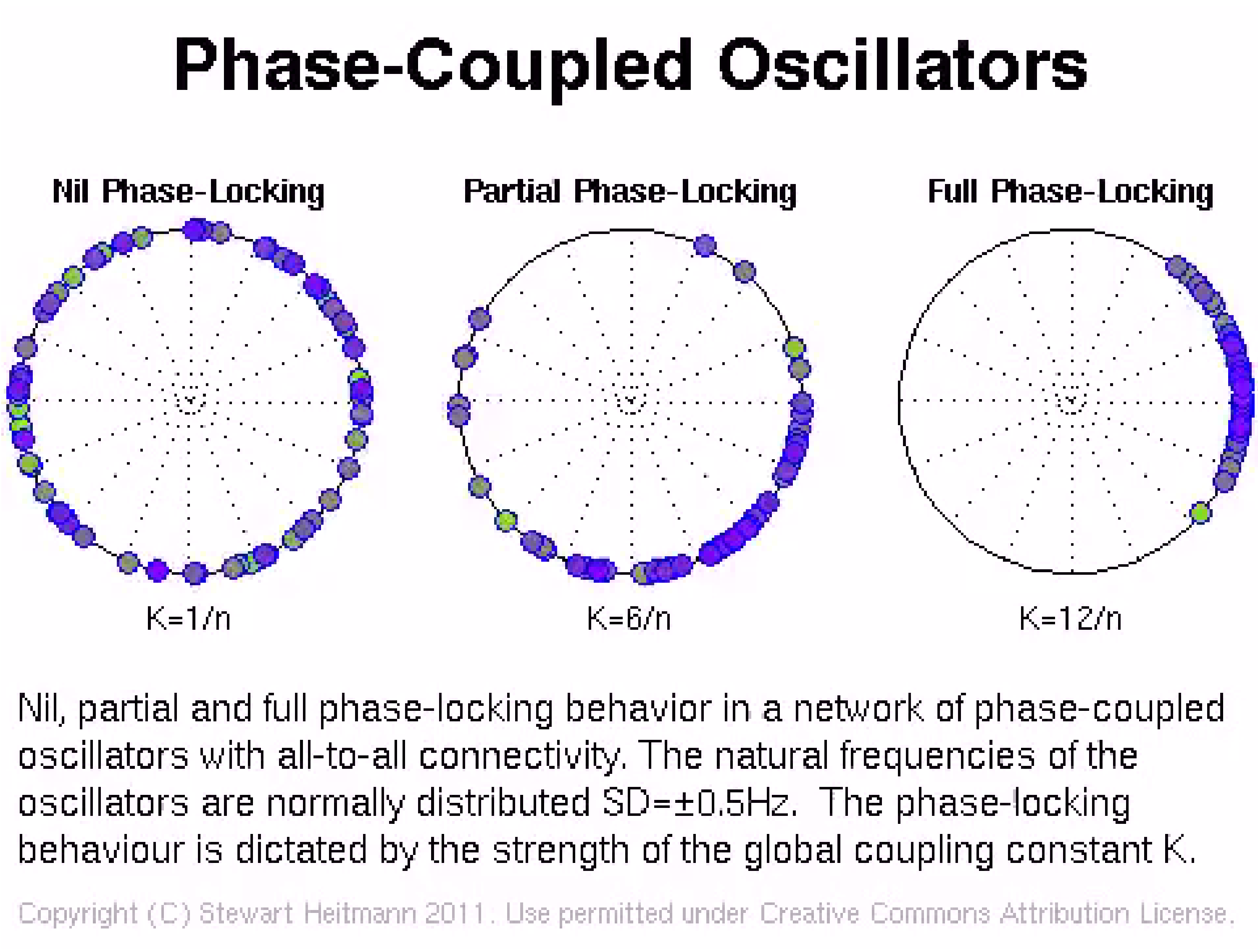
From: Mendoza et al., 2014, Synchronization in a semiclassical Kuramoto model.

Simulation results



Z : order parameter
t : time
N = 200 coupled oscillators
σ = 1
K = 2.5 (top curve),
0.5 (middle curve)
0 (bottom curve)

→ K=0 and K=0.5 (weak coupling) results in similar order parameter

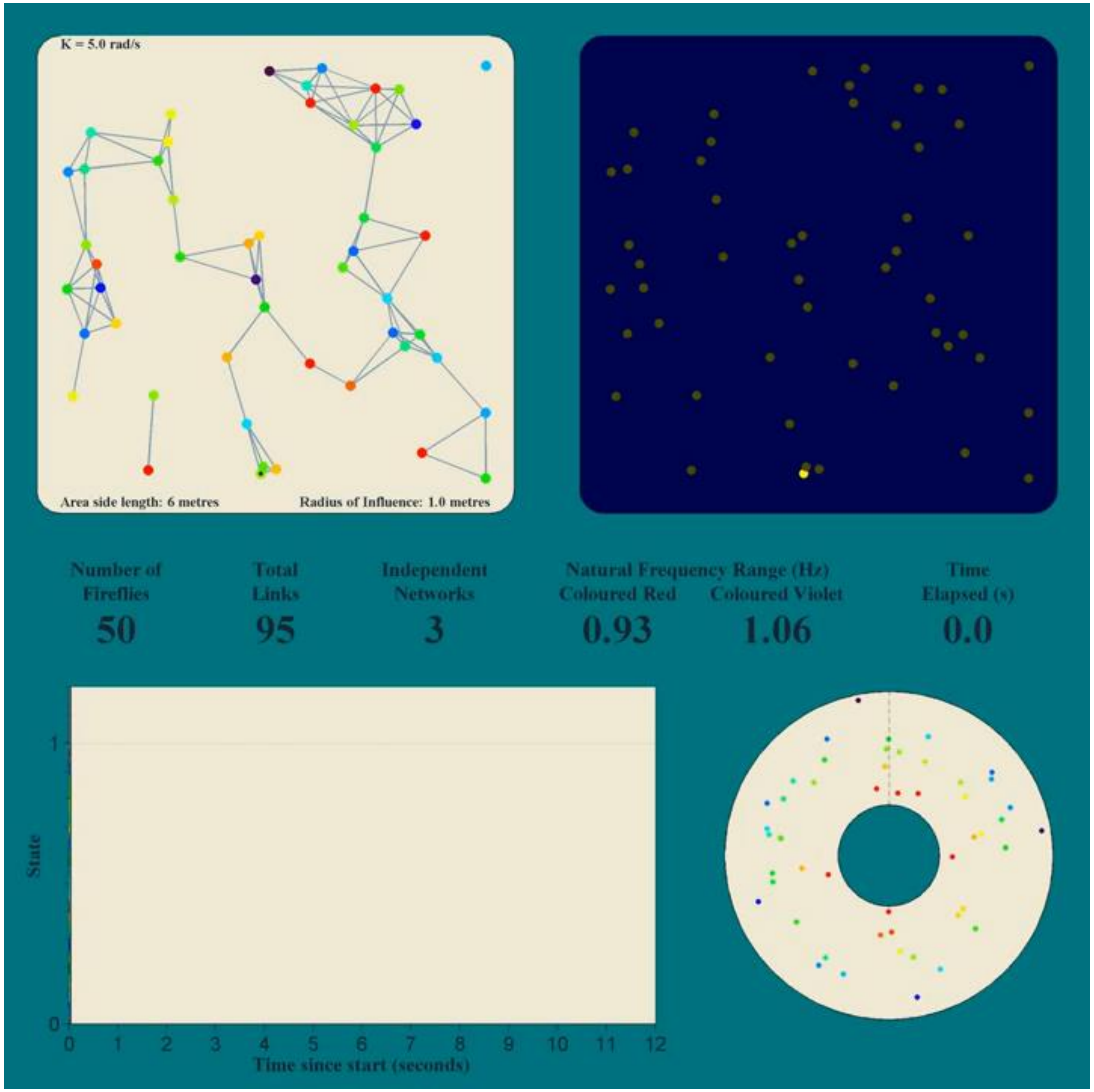


Phase-Coupled Oscillators

Nil, partial and full phase-locking behavior in a network of phase-coupled oscillators with all-to-all connectivity. The natural frequencies of the oscillators are normally distributed SD=±0.5Hz. The phase-locking behaviour is dictated by the strength of the global coupling constant K.

https://www.youtube.com/watch?v=9zrOoVlN8tg

Outlook: Kuramoto model on networks.



K = 5.0 rad/s

Area side length: 6 metres

Radius of Influence: 1.0 metres

Number of Fireflies: 50

Total Links: 95

Independent Networks: 3

Natural Frequency Range (Hz) Coloured Red: 0.93

Natural Frequency Range (Hz) Coloured Violet: 1.06

Time Elapsed (s): 0.0

The all-to-all coupling considered originally by Kuramoto can be trivially generalized to any connectivity structures by introducing other coupling forms (via (weighted) adjacency matrices, graphs, etc.)

This allows for the study of the synchronization properties of a variety of real-world systems for which interactions between constituents are better described as a complex networks.

https://www.youtube.com/watch?v=hzRhdUkZc-s

Noise in the discrete Kuramoto model

- The KM with the above defined noise:

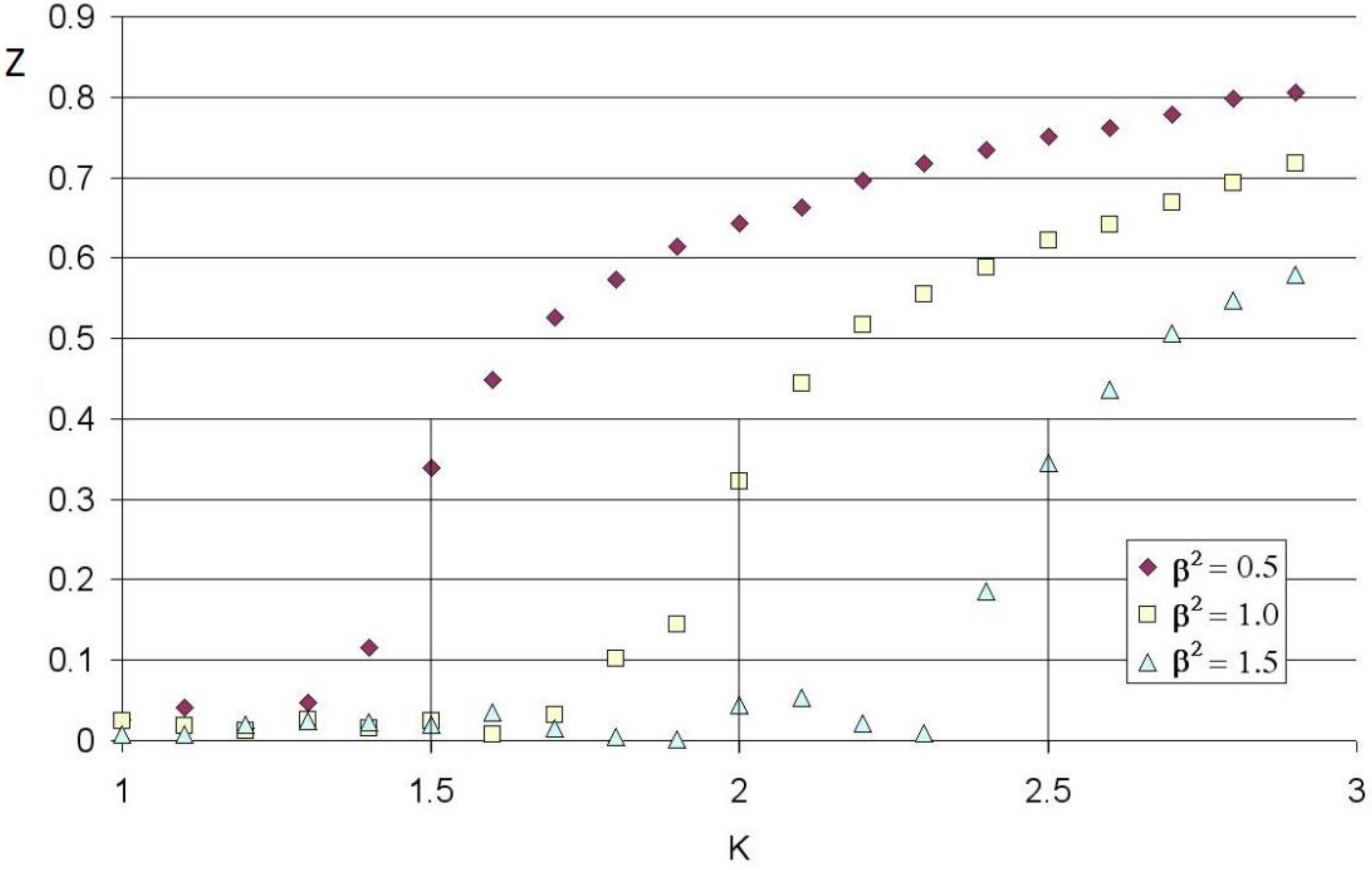
$$\frac{d\phi_i}{dt} = \omega_i + \frac{K}{N}\sum_{j=0}^{N-1} \sin\left(\phi_j - \phi_i\right) + \xi_i$$

- Or in other form:

$$\frac{d\psi_i}{dt} = \omega_i + KZ\sin(\theta - \psi_i) + \xi_i$$

- ξ: a random value chosen from a normal (Gaussian) distribution of mean zero and width $\beta^2/\Delta t$, where
- β^2 defines the strength of the noise, and
- Δt is the time of the time-steps used in the simulations

Simulation results with white noise introduced to the discrete KM



N=5000

The dependency of the magnitude of the order parameter Z on the coupling K in presence of noise. β^2 sets the strength of the noise. From theoretical results K_C is predicted to occur at $\beta^2 + 1$, shown as three vertical lines at 1.5, 2.0, and 2.5.

From: Bryan C. Daniels: Synchronization of Globally Coupled Nonlinear Oscillators: the Rich Behavior of the Kuramoto Model, Fig 4.2.