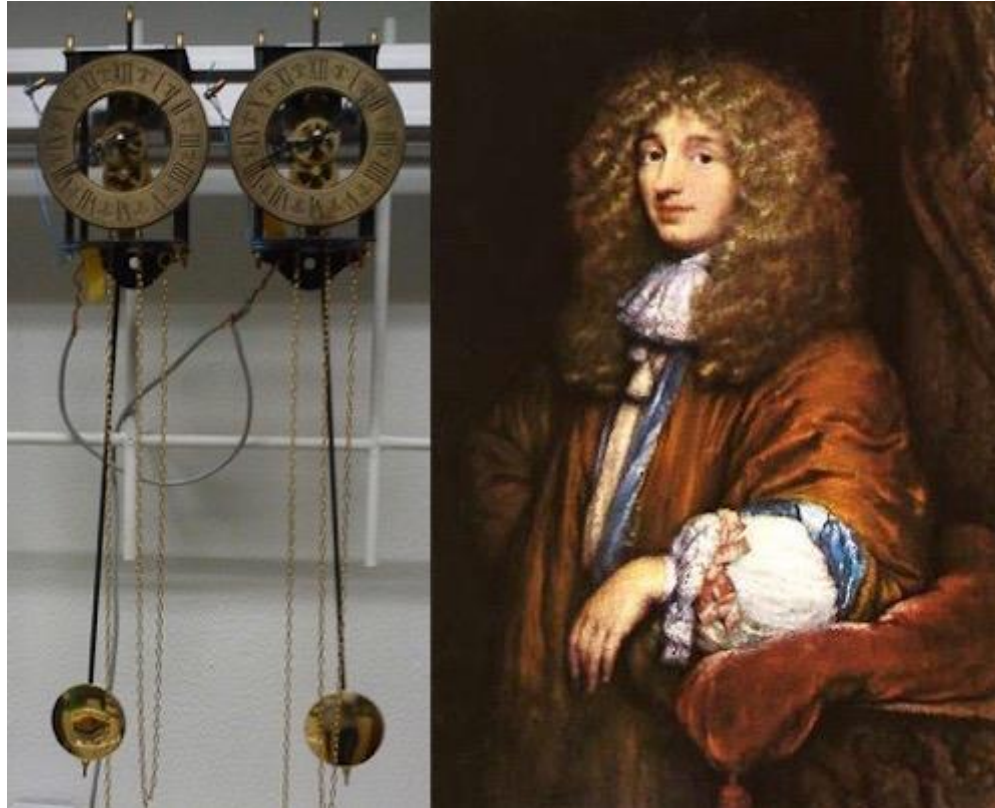


Biological synchronization

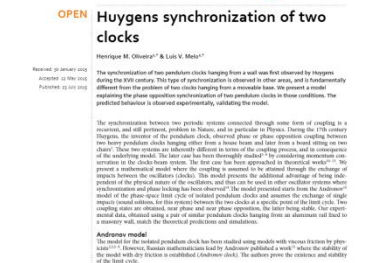
Historical background;
Kuramoto model;
Integrate and fire models

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*



SCIENTIFIC REPORTS



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.

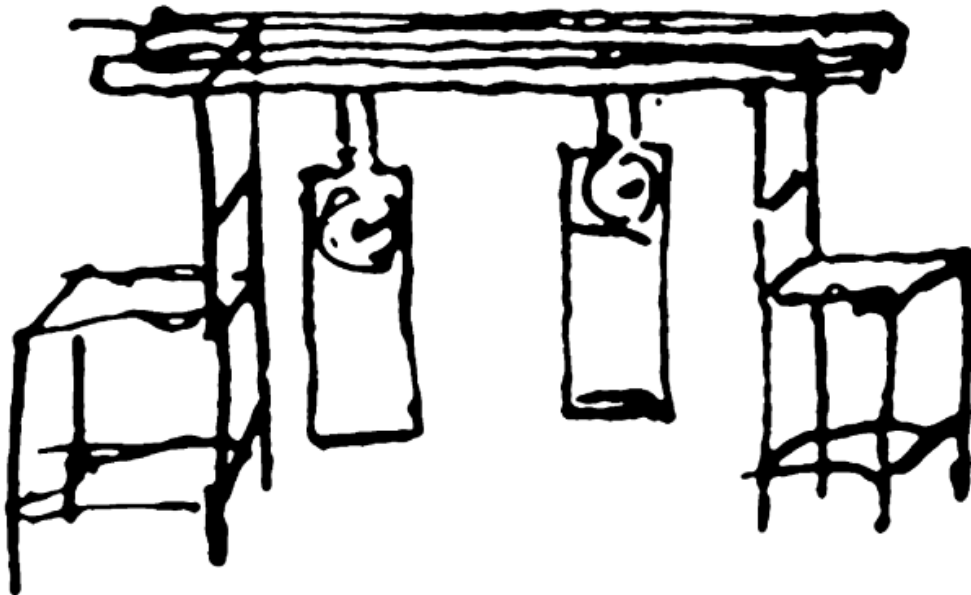
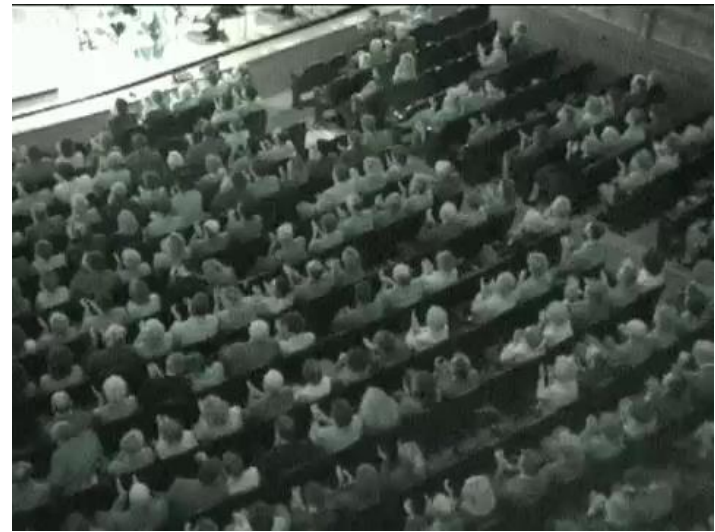


Figure 1.2. Original drawing of Christiaan Huygens illustrating his experiments with two pendulum clocks placed on a common support.

Then, until the 20th century,
only some isolated
observations appeared

- 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>



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

The symbolic example: fireflies in Southeast Asia

- For 300 years, Western travelers to Southeast Asia had been returning with tales of enormous congregations of fireflies blinking on and off in unison, stretching for miles along the riverbanks.
- Often written in the romantic style (travel books)
- provoked widespread disbelief

“Some twenty years ago I saw, or I thought I saw, a synchronal or simultaneous flashing of fireflies. I could hardly believe my eyes, for such a thing to occur among insects is certainly contrary to all natural laws.”

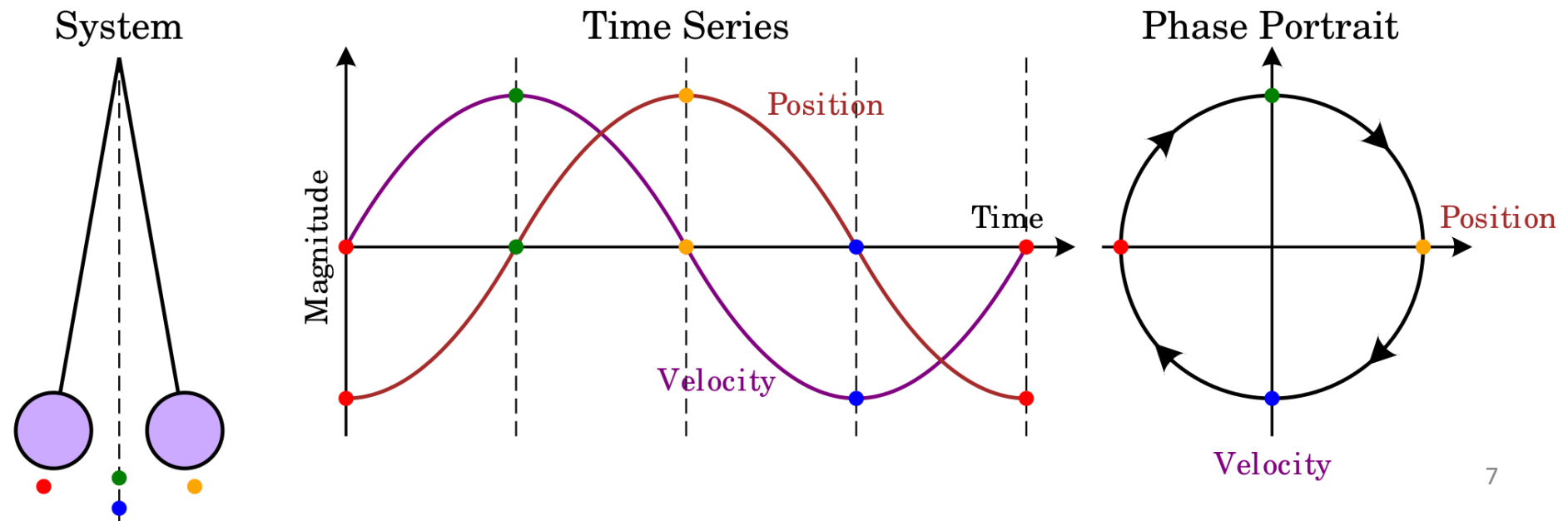
Philip Laurent in the journal Science, 1917

- Solution:
“The apparent phenomenon was caused by the twitching or sudden lowering and raising of my eyelids. The insects had nothing whatsoever to do with it.”

- Between 1915 and 1935 Science published 20 other articles on the firefly-phenomena:
 - Some: Fleeting coincidence
 - Others: peculiar atmospheric conditions of exceptional humidity, calm, or darkness
 - Few: there must be a “maestro”
- Only in the late 1960s, the pieces began to fall into place
 - One clue: Fireflies also flash is *rhythm* (constant tempo) – basically everybody missed it
 - Biologist John Buck and wife Elisabeth: collected some insects and took them to their hotel room, later laboratory

What is an “oscillator”?

- **Definition**: An oscillator is any system that executes periodic behavior.
 - A swinging pendulum: returns to the same point in space at regular intervals; its velocity also rises and falls with clockwork regularity
 - Their trajectories in the phase space are closed curves



Synchronization of coupled oscillators

Definition: Two or more oscillators are said to be coupled if some physical or chemical process allow them to influence one another

- Fireflies communicate with light
- Heart cells pass electrical currents back and forth
- Two pendulum clocks coupled through a common support

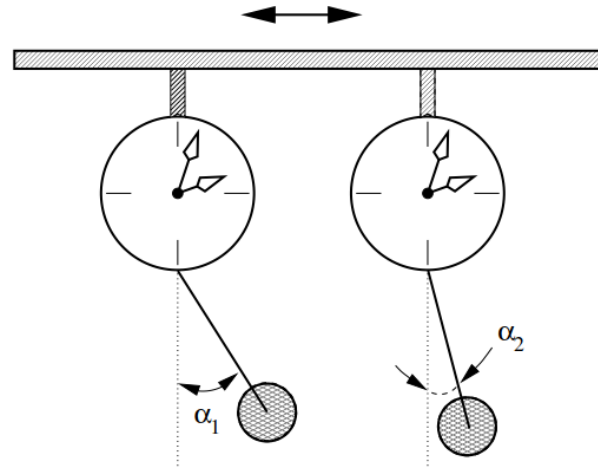
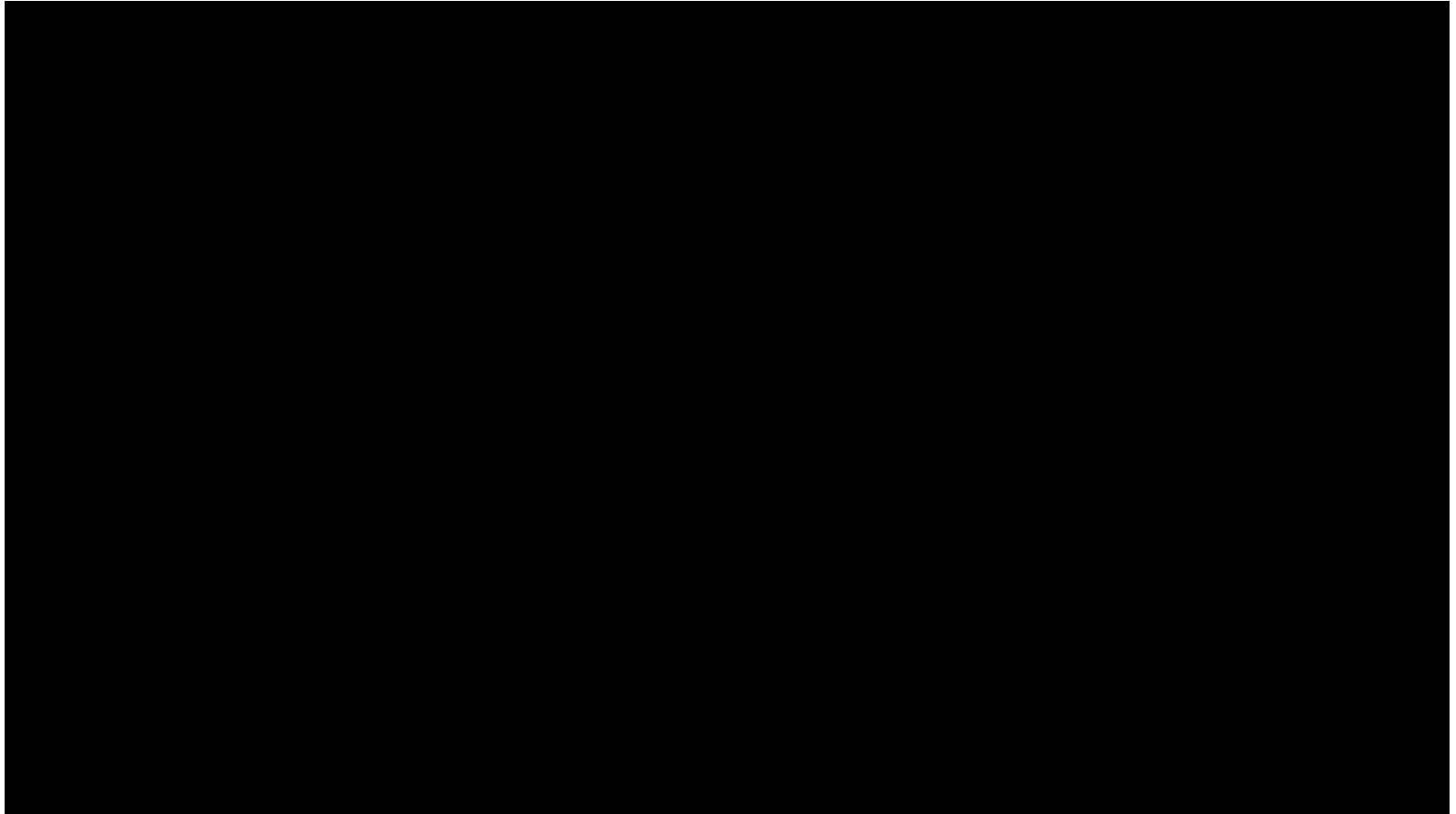


Figure 1.8. Two pendulum clocks coupled through a common support. The beam to which the clocks are fixed is not rigid, but can vibrate slightly, as indicated by the arrows at the top of the figure. This vibration is caused by the motions of both pendula; as a result the two clocks “feel” the presence of each other.

Definition: Synchronization: The spontaneous harmonization of units executing periodic behavior

- Coupled oscillators with nonlinear interaction
- It is a sort of *spontaneous order*

Oscillating metronomes – a demonstration



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

First models of biological oscillators

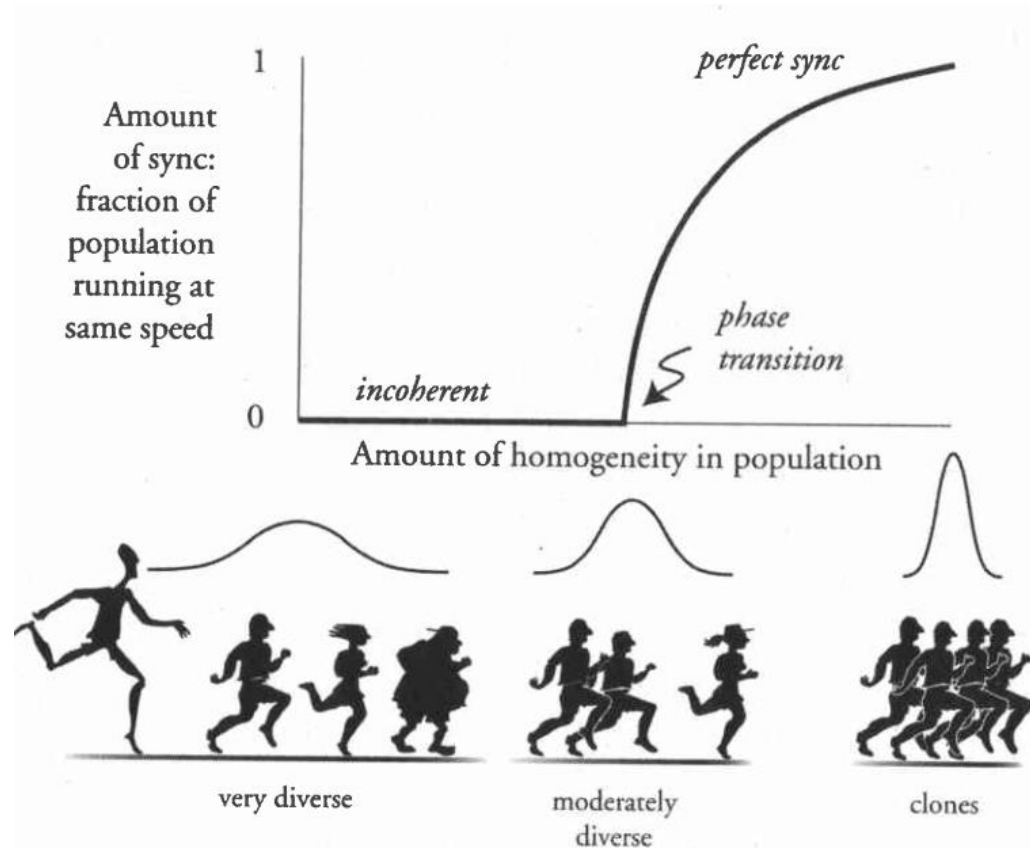
- Arthur Winfree, late 1960s
 - Ignored *all* biological differences and focused on the only common things: the ability to *send* and *receive signals*
 - Complication: both of these are often a function of phase
 - “Influence function” – what signal it sends
 - “Sensitivity function” – how an oscillator 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)

Winfree's model - continuation

- Assumed that the oscillators are globally coupled
- Instead of solving the differential equations, he used computer models (“experiment”)
 - For some sensitivity-influence function pairs he always got incoherence
 - For other sensitivity-influence function pairs he always got synchronicity
- Another aspect: the distribution of natural frequencies
 - Very diverse: no synch
 - Bit more diverse: same
 - There is a threshold

Phase transition

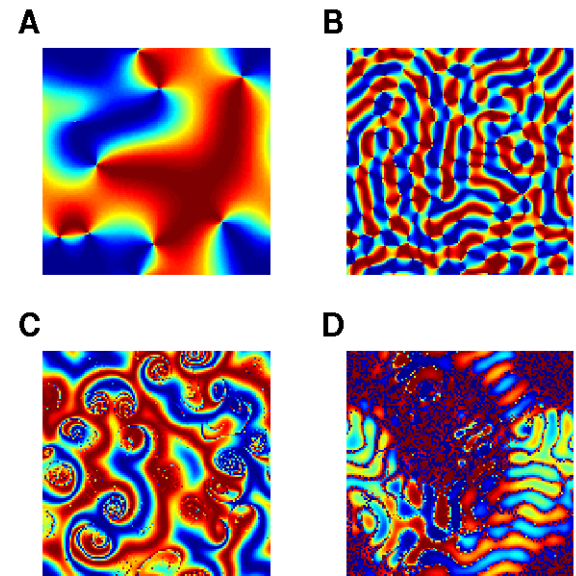
- Connection between nonlinear dynamics and statistical physics



Kuramoto model



- 1975: solved a simpler, more abstract version of Winfree's model
- Replaced Winfree's influence and sensitivity function with a *sine* function: highly symmetrical rule for Winfree's concept of "frequency pulling"
 - (analogy: jogging friends)
- The original formulation was motivated by the behavior of systems of chemical and biological oscillators
- Later it has found widespread applications in other fields too (neuroscience, physical systems, etc.)
- The model makes several 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.



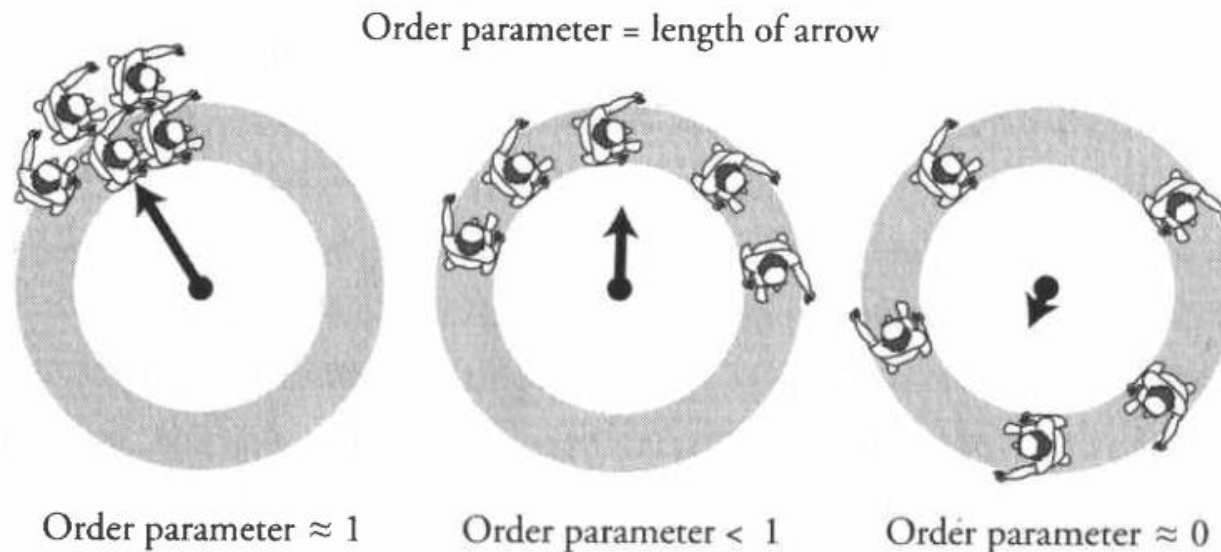
Distinct synchronization patterns in a two-dimensional array of Kuramoto-like oscillators with differing phase interaction functions and spatial coupling topologies. (A) Pinwheels. (B) Waves. (C) Chimeras. (D) Chimeras and waves combined. Color scale indicates oscillator phase.

Kuramoto model with the runner analogy

- Locations are indistinguishable
- Interaction rule:
 - each runner looks at all the others (),
 - computes a velocity correction relative to each,
 - Calculates their average
- The runners can start at random places

Order parameter:

- Quantifies the degree of synchronization
- Between 0 and 1
- Depends on the relative position of the runners
- Kuramoto's prediction: in the long run the order parameter always tends to a certain value



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
 - $\nu_i = \frac{1}{T_i}$: frequency
 - $\omega_i = \frac{2\pi}{T_i}$: natural frequency
- One oscillator (an oscillator without interaction):

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

The Kuramoto model in mean field approximation

- N coupled oscillators interacting with each others pairwise :

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

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

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

- K : strength of the coupling
- If $K > 0 \rightarrow \Gamma$ minimizes the phase difference
- The spatial position of the oscillators is irrelevant \rightarrow mean field appr.

The Kuramoto model in mean field approximation

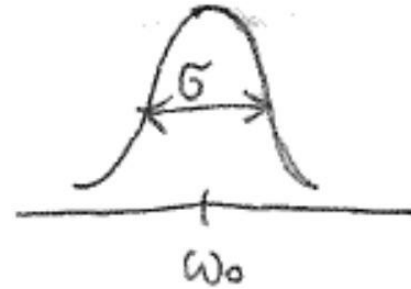
- The basic formula of the KM with MF approximation:

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

- How do such oscillators synchronize?
- The interplay between the coupling strength and the distribution of the natural frequencies determines how many oscillators are synchronized, and, hence, how strong the mean field is.
- 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:

$$\Psi_i := \phi_i - \omega_0 t$$

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

(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):

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

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

Defining the order parameter – cont.

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

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

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

$$K_C = \frac{2}{\pi \cdot g(\omega_0)} \quad (\omega_0 \text{ is the mean frequency of the } g(\omega) \text{ frequency distribution})$$

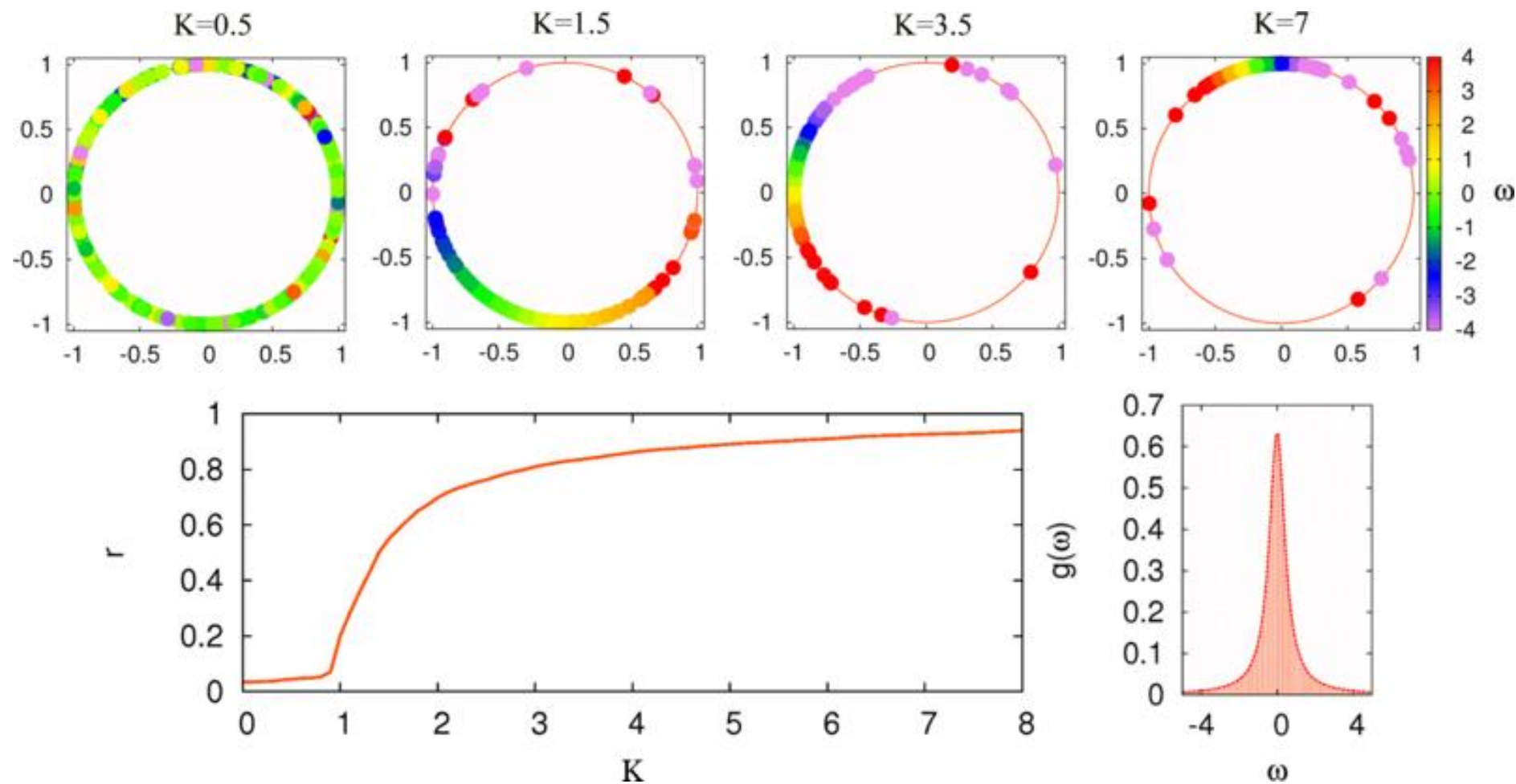
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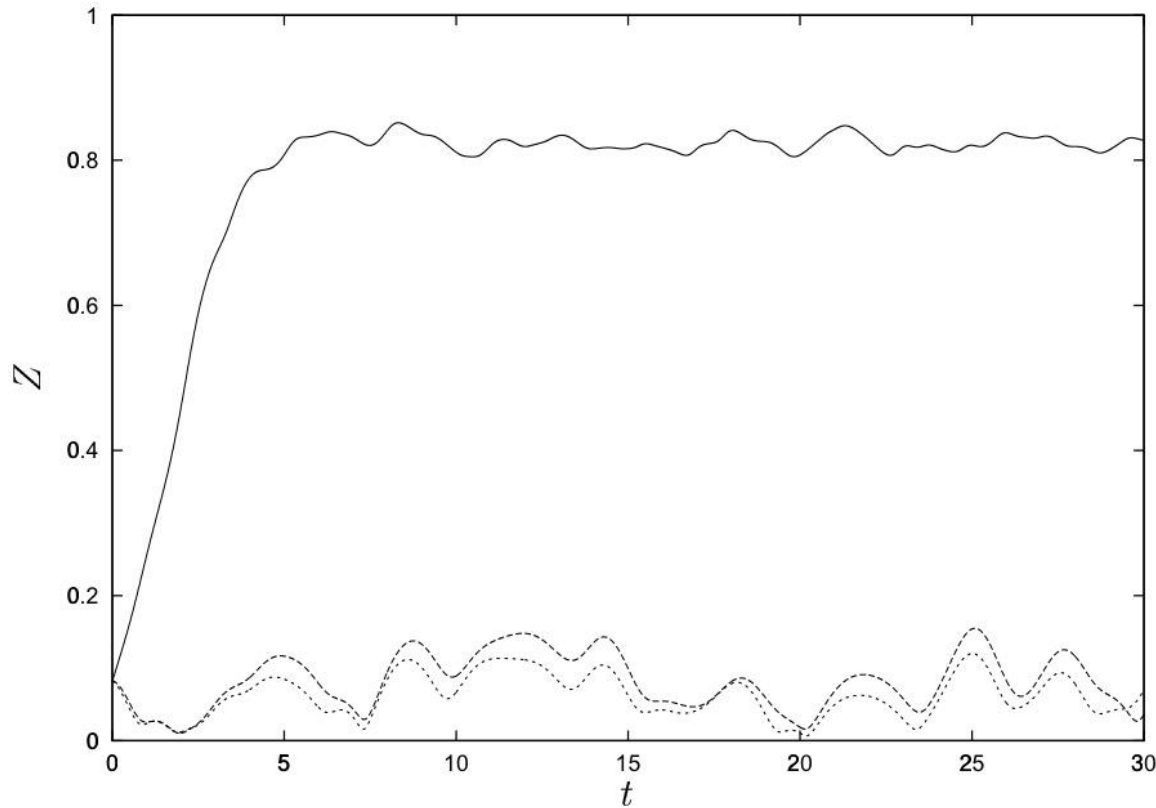
(ω_0 is the mean frequency of the $g(\omega)$ frequency distribution)





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 $K_c = 1$.

Simulation results



Z : order parameter

t : time

$N = 200$ coupled oscillators

$\sigma = 1$

$K = 2.5$ (top curve),
0.5 (middle curve)
0 (bottom curve)

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

For the region where Z is constant

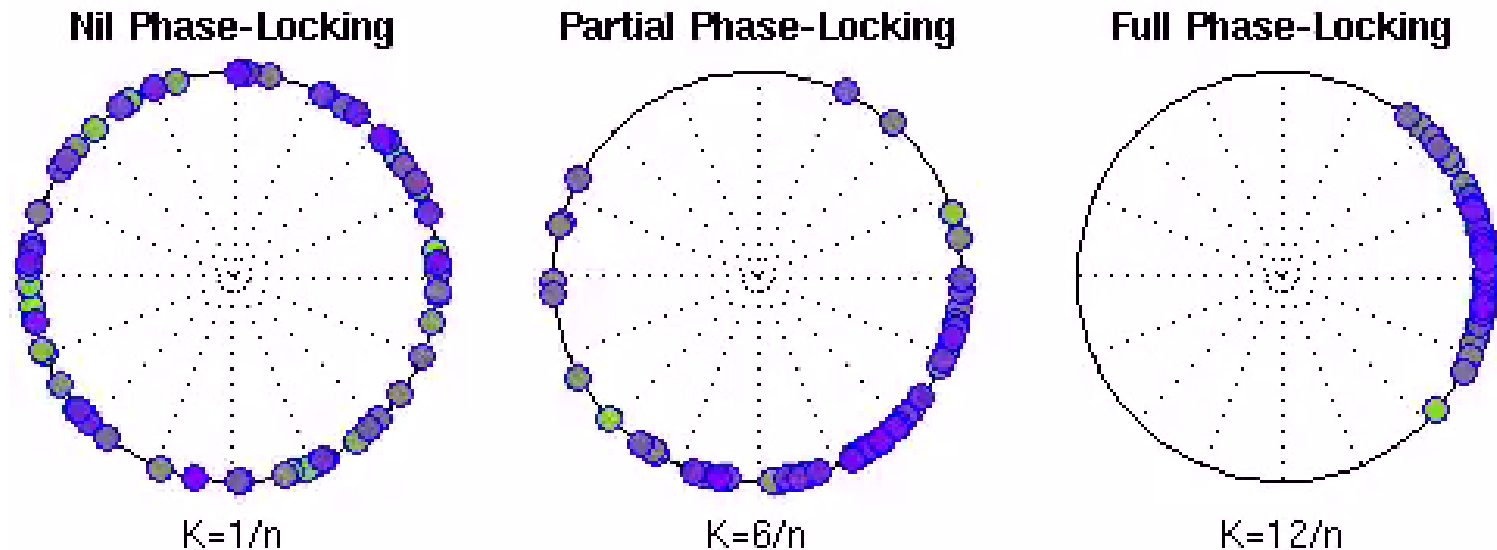
- According to Kuramoto's analysis, based on the definition of the order parameter and on the time evolution of the phases, we get:

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

- A set of one-dimensional uncoupled system!
- In other words: the particle is just interacting with the mean-field (produced by the average)
- But for this you need Z to be independent of t
 - **Q:** How can it be, given that there are drifting oscillators?
($Z < 1 \rightarrow$ the synchronization is not perfect \rightarrow there are “drifting” oscillators)
 - **A:** The oscillators form a stationary distribution on the circle

$$\left(\text{Original form was: } \frac{d\psi_i}{dt} = \omega_i + \frac{K}{N} \sum_{j=0}^{N-1} \sin(\psi_j - \psi_i) \right)$$

Phase-Coupled Oscillators



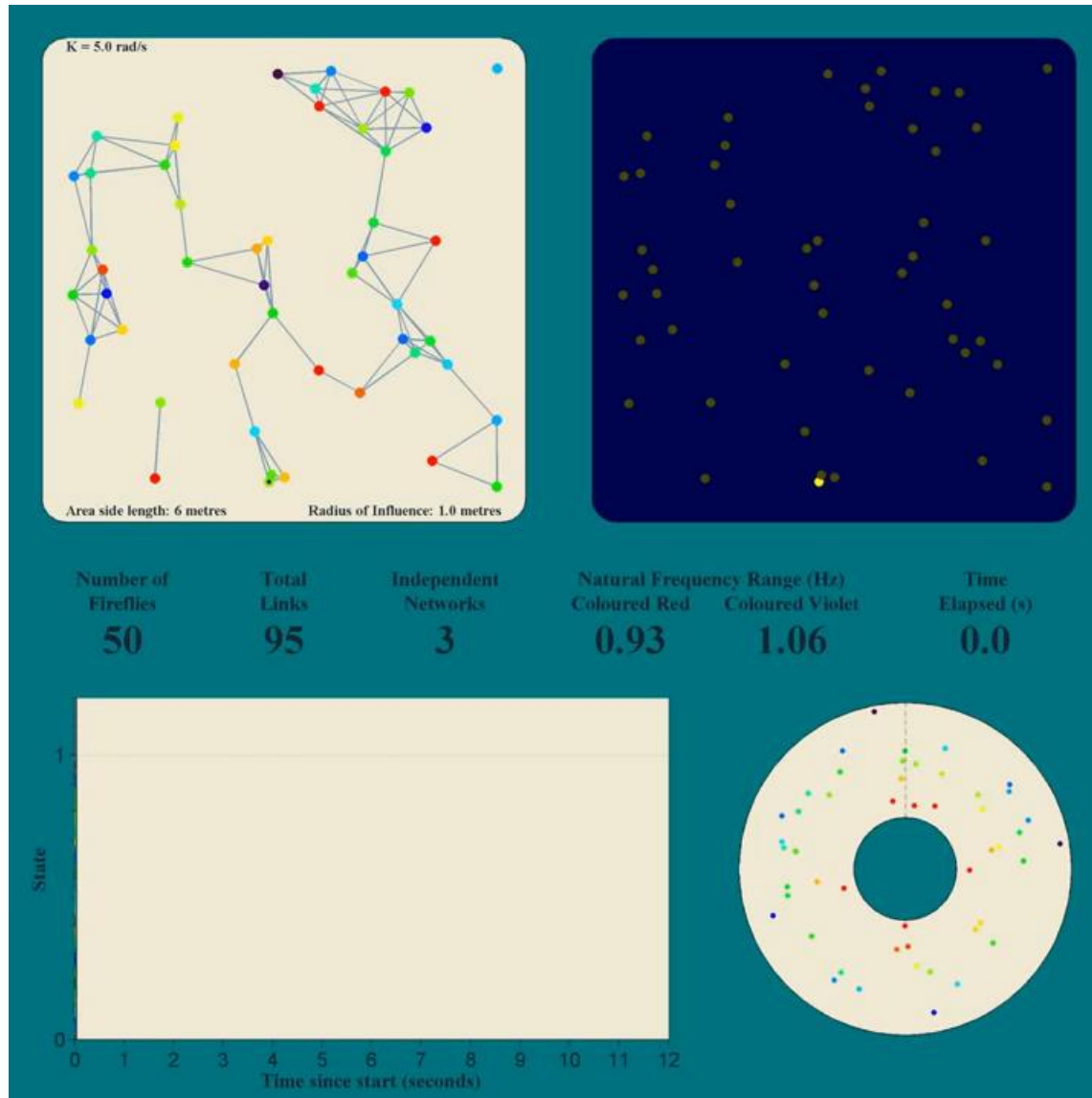
Nil, partial and full phase-locking behavior in a network of phase-coupled oscillators with all-to-all connectivity. The natural frequencies of the oscillators are normally distributed $SD=\pm 0.5\text{Hz}$. The phase-locking behaviour is dictated by the strength of the global coupling constant K .

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Outlook: Kuramoto model on networks.

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 are better described as a complex networks.



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

Distance dependency

- In some cases dependency on the distance is more realistic than MF
- Assumptions:
 - Oscillators sit on a grid
 - $r_{i,j}$ is the distance between oscillators i and j
 - α is an exponent determining the strength of the distance dependency
 - η is a renormalizing factor
- The time evolution of the oscillator phases:

$$\frac{d\phi_i}{dt} = \omega_i + \frac{K}{\eta} \sum_{i \neq j} \frac{\sin(\phi_j - \phi_i)}{r_{i,j}^\alpha}$$

- Can not be handled analitcly
- Dependency on α :
 - $\alpha = 0$: no dependency, gives back the mean field approach
 - $\alpha \rightarrow \infty$: the interaction decays fast, interaction only with the first neighbor

Distance dependency

$$\frac{d\phi_i}{dt} = \omega_i + \frac{K}{\eta} \sum_{i \neq j} \frac{\sin(\phi_j - \phi_i)}{r_{i,j}^\alpha}$$

- In most physically realistic case $\alpha = d - 1$
- If $\alpha > d$, then the connection term is finite for $\forall N$:

$$\left| \sum_{i \neq j} \frac{1}{r_{i,j}^\alpha} \sin(\phi_j - \phi_i) \right| \leq \sum_{i \neq j} \frac{1}{r_{i,j}^\alpha} < \infty$$

- If $\alpha \leq d$, then
 - If $N \rightarrow \infty$ then for $\forall K > 0$: synchronization
- The tendency for synchronization can be stronger than in the MF case

Noisy oscillators in the KM

- Noise is usually present in real-life systems
 - From internal sources (evaluation of influences, differences in states, etc.)
 - From external sources (perturbations of the environment, effects of other oscillators, etc.)
 - We unite these effects in one parameter ξ .
- Q: how random noise changes the synchronization behavior of the Kuramoto model?
 - Strong coupling: the system synchronizes
 - Big noise: desynchronizes the system
- Noise term ξ_i is defined as (white noise)

$$\langle \xi_i(t) \rangle = 0$$

$$\langle \xi_i(s) \xi_j(t) \rangle = 2D \delta_{ij} \delta(s - t)$$

- First condition: the time average of the noise acting on oscillator i is zero
- Second condition: the noise terms for different oscillators or different times are non-correlated
- The strength of the noise is set by the parameter D .

Noise in the discrete Kuramoto model

- The KM with the above defined noise:

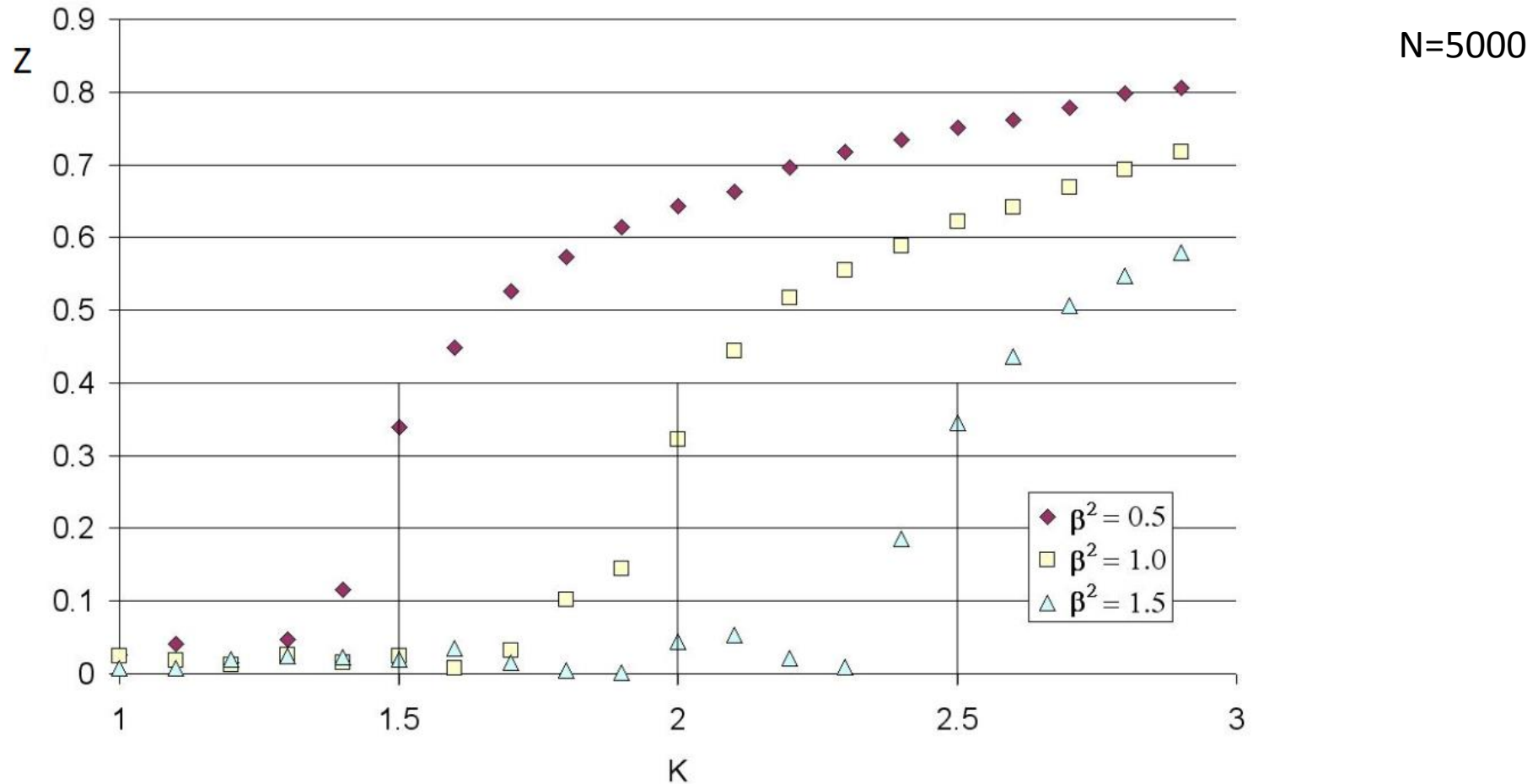
$$\frac{d\phi_i}{dt} = \omega_i + \frac{K}{N} \sum_{j=0}^{N-1} \sin(\phi_j - \phi_i) + \xi_i$$

- Or in other form:

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

- For running simulations of the Kuramoto model with noise, these equations are enough, since the noise term ξ can be simulated with a random number generator
- The correct form of ξ to use for each time-step is 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

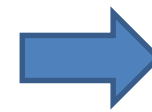


The dependency of the magnitude of the order parameter Z on the coupling K in presence of noise. β^2 sets the strength of the noise. From theoretical results K_c is predicted to occur at $\beta^2 + 1$, shown as three vertical lines at 1.5, 2.0, and 2.5.

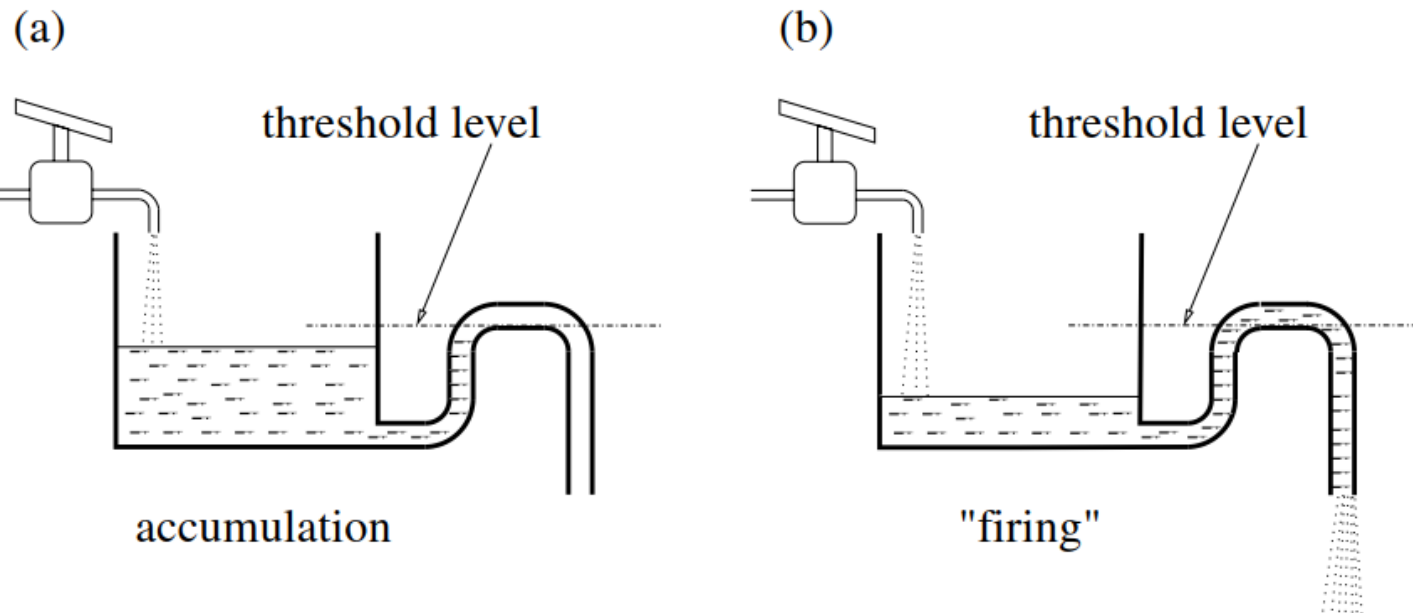
Relaxation oscillators

Basic feature: two time scales within each cycle

- A slow growth (linear or not)
- Fast resetting

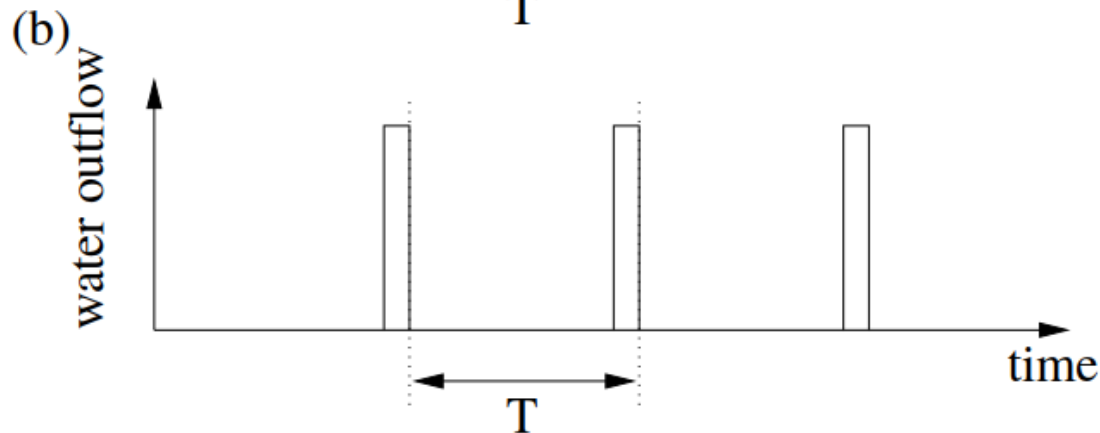
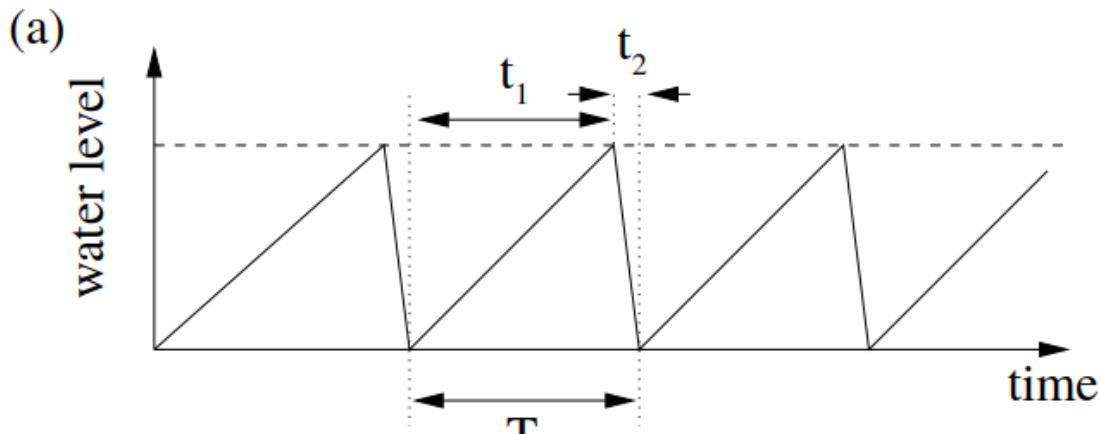
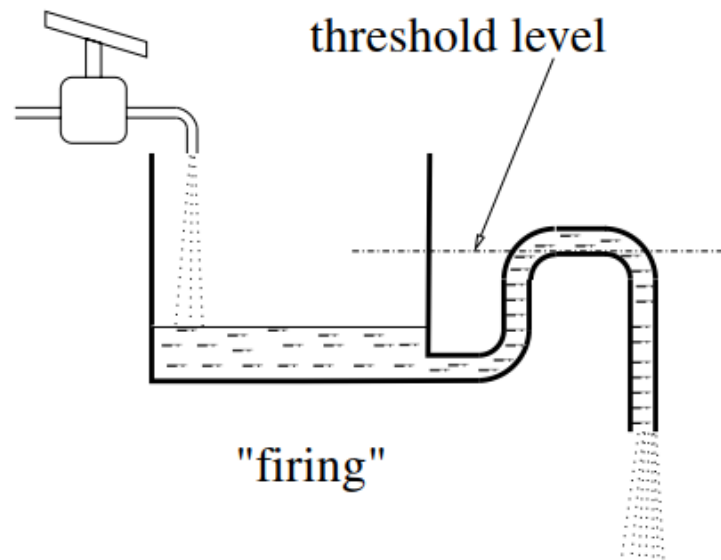
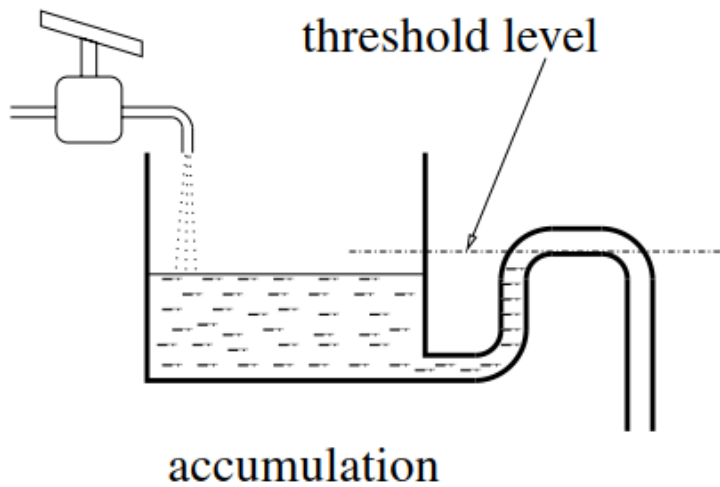


*“Integrate-and-fire” or
“accumulate and fire”*



The energy of the pump that provides a constant water supply is transformed into oscillations of the water level in the vessel.

Figure 2.12. Mechanical model of a relaxation (integrate-and-fire) oscillator. (a) The water slowly fills the vessel until the threshold value is reached; this part of the cycle can be denoted “integration”. (b) The water flows out through the trap and its level in the vessel quickly goes down: the oscillator “fires”.



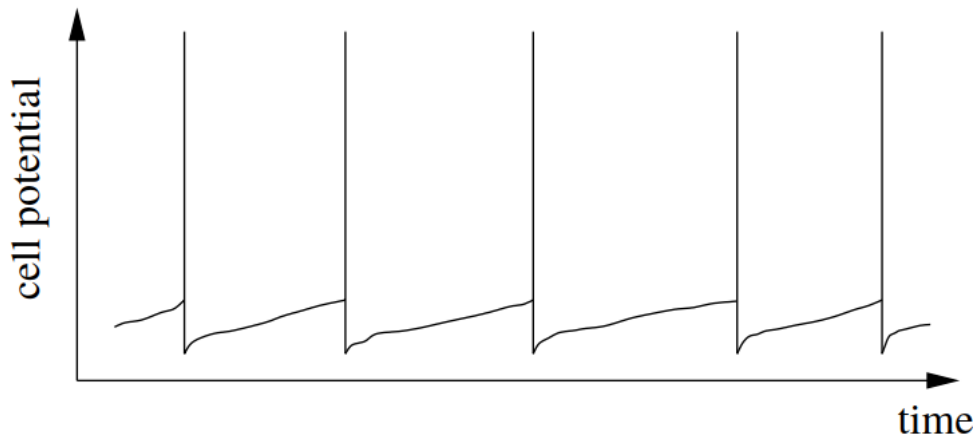
Time course of the mechanical integrate-and-fire (accumulate-and-fire) oscillator.

Water accumulates until it reaches the threshold level shown by a dashed line (a), then the water level is quickly reset to zero. The resetting corresponds to the pulse in the plot of the water outflow from the trap (b)

Integrate-and-fire oscillators are common in biology

- Heartbeat (Voltage pulses for cardiac cells)
- Light flash (fireflies)
- **Neurons:** if a current is injected into the cell, the electric potential (the voltage difference between the inside and outside of the neuron) is generally slowly changing, but occasionally it changes very rapidly producing spikes (action potentials) of about 2 *ms* duration.
 - Spike: when the cell potential reaches a threshold ≈ -50 mV
 - discharging of the cell
 - After discharging, the cell resets to about -70 mV.
- When a constant current is injected into the cell, the action potentials are generated at a regular rate; slow variation of the current alters the firing rate of the neuron
- This is how sensor neurons work: the intensity of the stimulus is encoded by the firing rate.

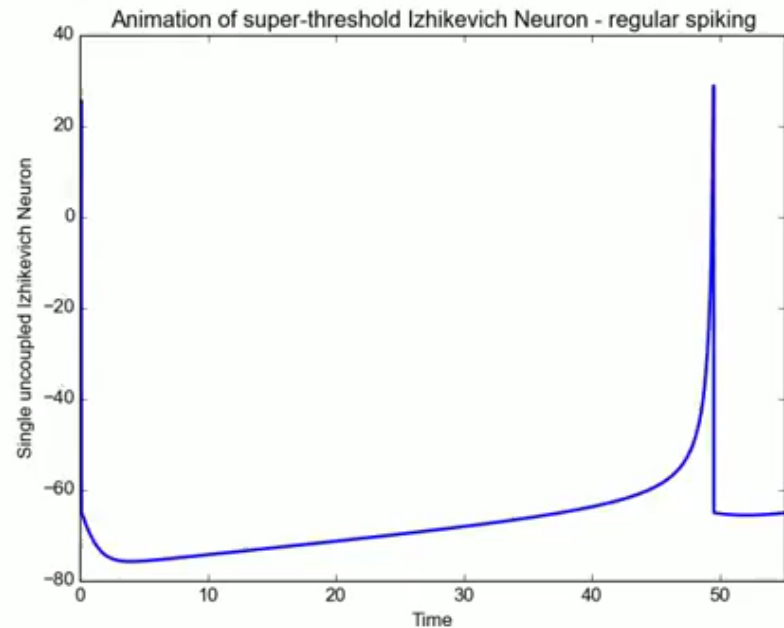
} *A cycle*



Intracellular potential in a neuron slowly increases towards the threshold level (≈ -53 mV in the particular example presented here) and then, after a short spike, resets.

Synchronization of integrate and fire (IF) oscillators with global coupling

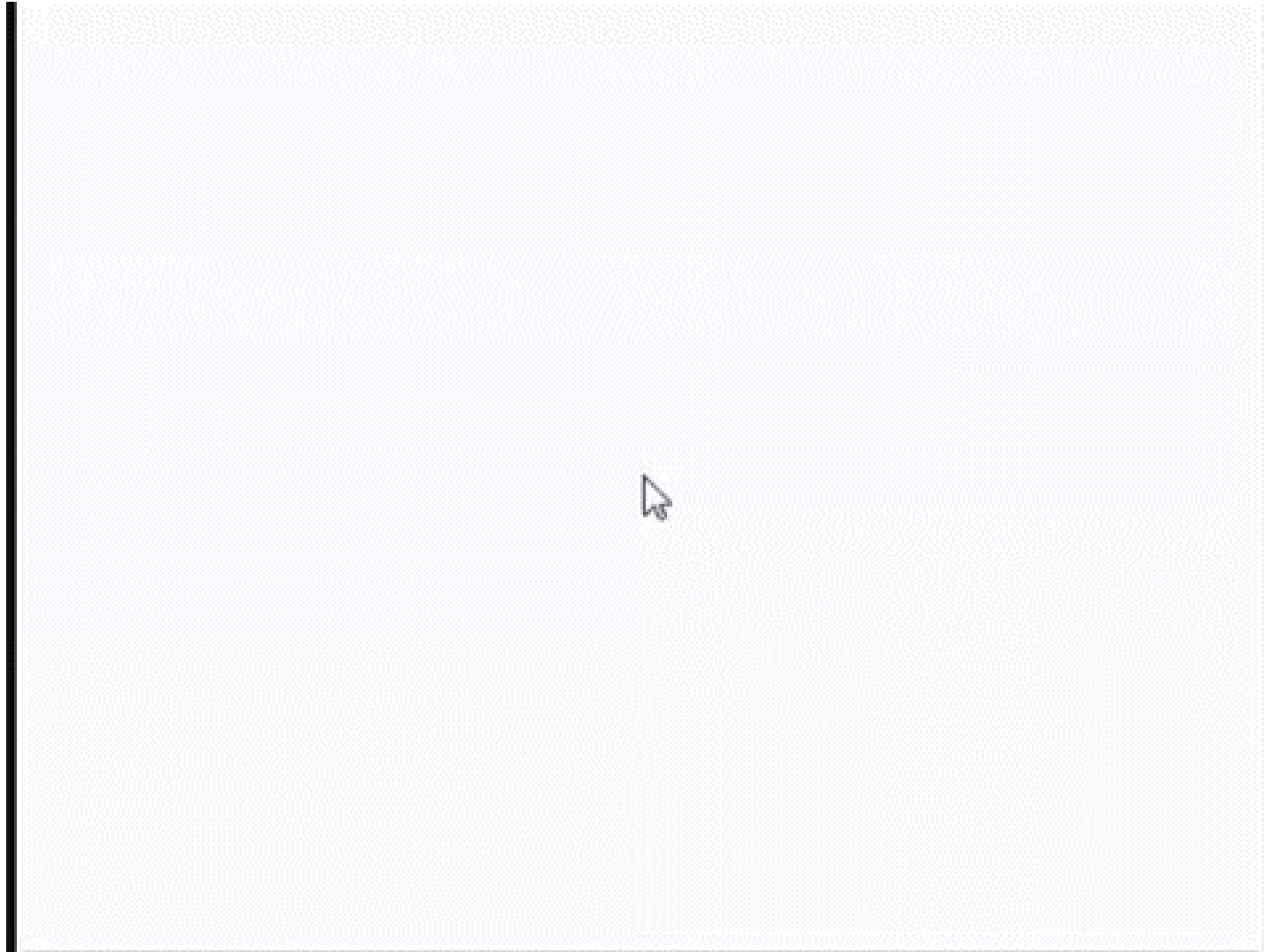
- A period of an IF
 - Monotonic increase up to a threshold value
 - When the threshold is reached, the oscillator relaxes to a basal level by firing a pulse to the other oscillators
 - A new period
- Synchronization is a central mechanism for information processing
 - Communication between brain areas
 - Integration and coordination of information
 - Binding effect
 - Etc.



<https://www.youtube.com/watch?v=JzJmLf5cB7s>

Samuele Bottani: Synchronization of integrate and fire oscillators with global coupling, Physical Review E, Vol. 54, 1996

An example: a certain neuron in the visual pathway



<https://www.youtube.com/watch?v=dsCltnAlh5k>

Model variations

- Models:
 - The nature of coupling (grid, global coupling, network, etc.)
 - Identical or non-identical oscillators
 - Firing amplitude, frequency
 - The nature of the state function (evolution function)
 - Convex / concave / linear
 - Nature of noise
 - Excitatory / inhibitory pulses
 - With or without transmission delay / fall time
- Q: What are the conditions for synchronization?
- What we will consider now:
 - Global all-to-all coupling
 - Identical oscillators
 - Convex, concave and linear
 - Without noise
 - Excitatory pulses
 - Without transmission delay and fall time

Describing one IF oscillator

- N IF oscillators, O_i ($i = 1, \dots, N$)
- Each represented by a (real) state variable $E_i \in [0, E_i^c]$
- E_i^c : threshold of the oscillators (identical); $E_i^c := 1$ (we choose the unit like this)
- ϕ_i : the phase of oscillator i , $\phi_i \in [0, 1]$

The free evolution of O_i is made up of two parts:

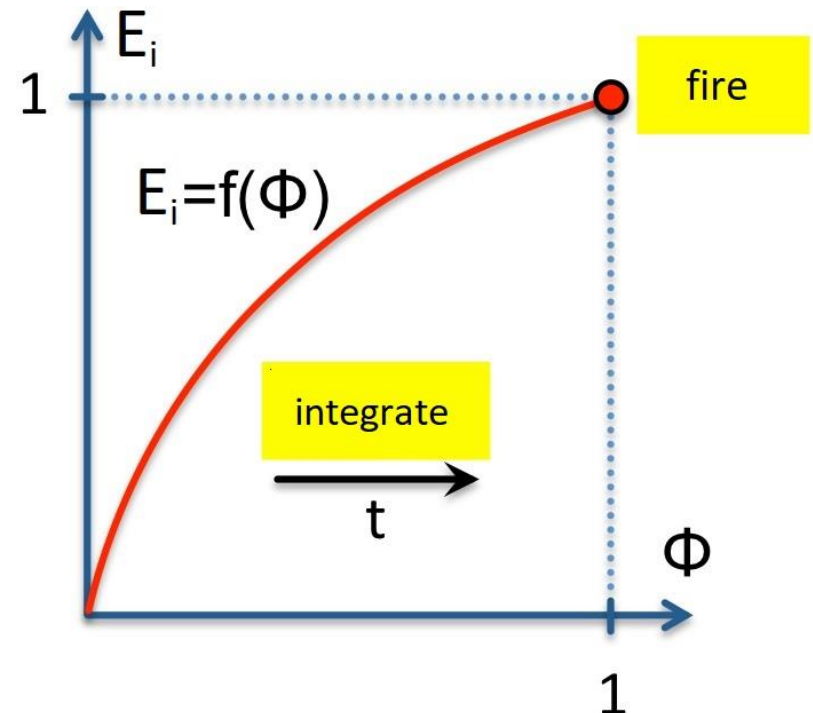
1. A charging/growth period during which E_i increases monotonically in time as long as it is below the threshold E_i^c according to a given free evolution function $E_i = f(\phi(t))$. (“integrate”)
2. A relaxation when the threshold is reached whereby E_i is reset to zero and a new growth period starts again. (“fire”)

$$E_i = 0 \leftrightarrow \phi_i = 0$$

$$E_i = 1 \leftrightarrow \phi_i = 1$$

that is

$$f(0) = 0 \text{ and } f(1) = 1$$



Assumption: the characteristic time for the relaxation is very short compared to the charging period; “instantaneous”.

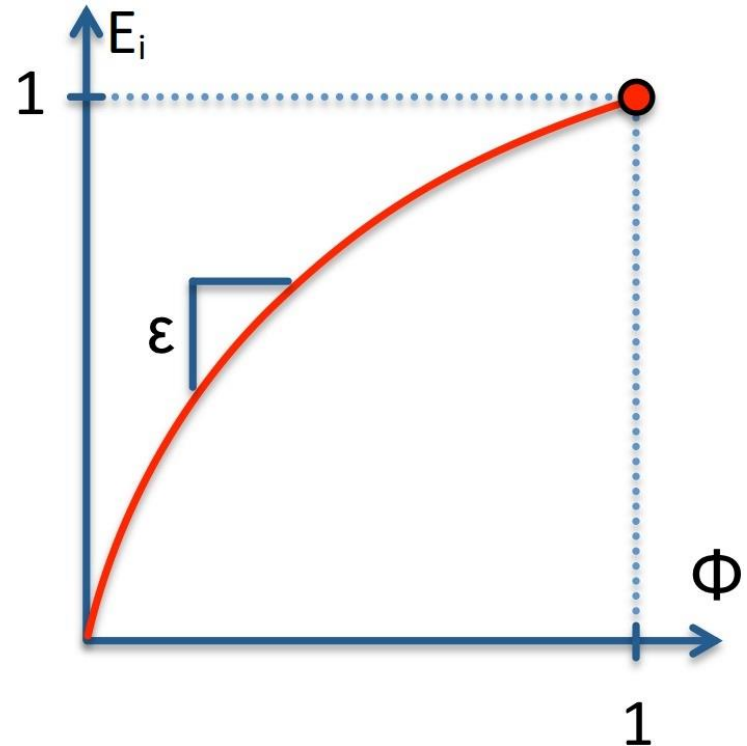
Interaction

- If the state (energy level) of an oscillator O_i reaches its threshold ($E_i^c = 1$), then it fires
- This firing increases the state (energy level) of its neighbors with ε
 - $E_j \rightarrow E_j + \varepsilon$, or, if
 - $E_j + \varepsilon > 1$, then $E_j = 1$
- The pulse strength depends on the number of oscillators that fire together and obey an additivity principle
- We assume direct additivity ($n \cdot \varepsilon$, where ε is the pulse strength of the firing oscillator)

Excitatory \rightarrow Increases E_j , and thus anticipating the firing. (this is the type we consider)

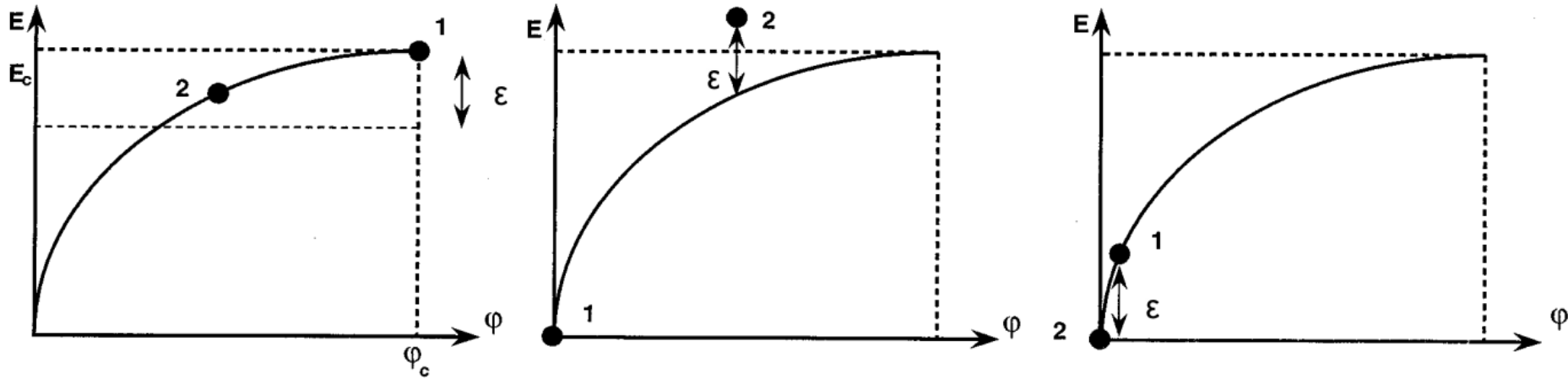


Inhibitory \rightarrow Decreases E_j , and thus delaying the firing.



Two oscillators firing in the same avalanche

How can they synchronize? – the problem



The oscillator (1) is at the threshold; the oscillator (2) is below the threshold at a distance smaller than ε , which is the pulse strength of a single firing.

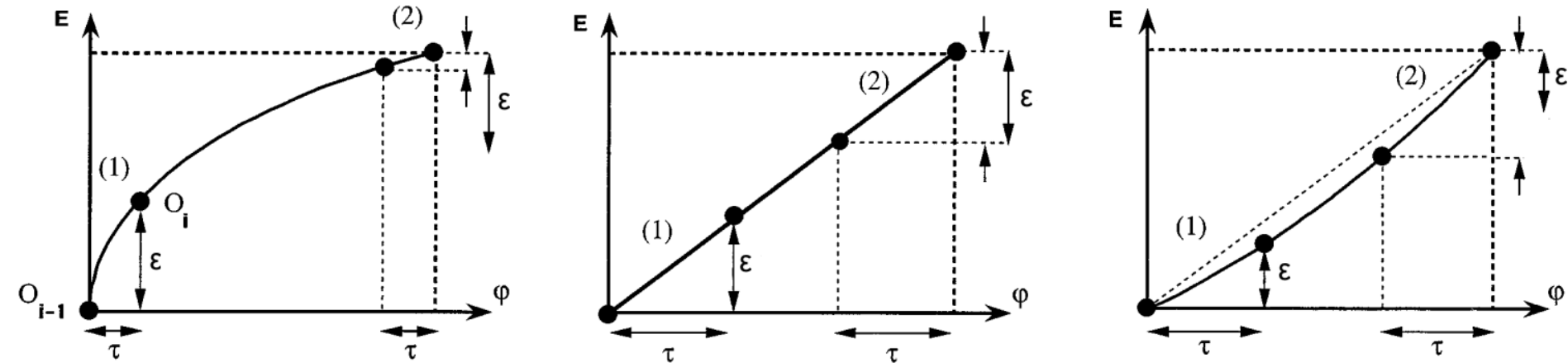
The oscillator (1) has relaxed and the emitted pulse has pushed the oscillator (2) above the threshold and thus makes it fire.

Without absorption the firing of oscillator (2) has pushed (1) away from the origin: the oscillators remain de-phased.

Avalanches and the absorption rule

- **Avalanche:** a cascade of firings until no pulse is sufficient enough to bring another oscillator above threshold.
 - It may occur when an oscillator reaches the threshold: depending on the other oscillator states the transmitted pulse may cause some other oscillators to exceed the threshold and fire. Possibly the new pulses may themselves cause further relaxations and such a cascade of firings.
 - In our model the firing is very fast compared to the integration period, so during an avalanche the continuous drive of the oscillators is not acting.
 - Connection to SOC
- **Absorption rule:** is the assumption that the oscillators that relax during the same avalanche are insensitive to the further pulses in the avalanche.
 - This rule corresponds the *refractory time* of the oscillators immediately after their relaxation.
- **Synchronization** (definition): oscillators get in phase (get synchronized) when they fire in a same avalanche. (“they are absorbed in a synchronized group of oscillators with identical phase”)

Synchronization with various $f(\phi)$ -s



(Left:) Synchronization without absorption for identical *convex* oscillators. Oscillator (1): Immediately after their avalanche two oscillators O_i and O_{i-1} have a gap between their states E of value ε . τ is the gap between the phases of O_i and O_{i-1} , which does not change during the free evolution between firings. Oscillator (2): When the most advanced oscillator is at the threshold the gap between their phases has not changed but the gap between their state variables has decreased due to the convexity. The second oscillator is at a distance of the threshold smaller than d : the oscillators avalanche again together.

(Middle:) Synchronization without absorption for identical *linear* oscillators. Same as for the convex case, but due to the linearity the gap between the state values does not change and is exactly equal to ε : the oscillators still avalanche together.

(Right:) Effect of *concavity*. The gap between the oscillator states increases as the pair approaches the threshold.

Statements

(1) It has been shown that a population of

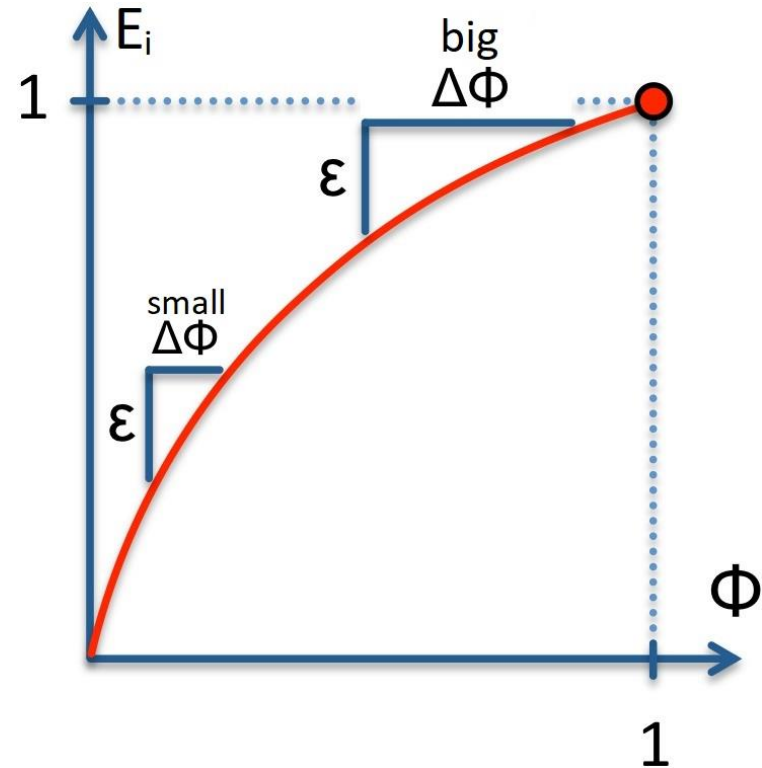
- Identical
- integrate and fire oscillators
- with convex evolution function
- globally coupled by
- exciting pulses
- added to the state variables

Synchronize completely¹

(2) In the presence of absorption, all the three types of evolution functions

- Convex
- Concave
- Linear

Synchronize, if N is big.²



¹Mirollo and Strogatz, 1990

²Bottani, 1996