Biological synchronization

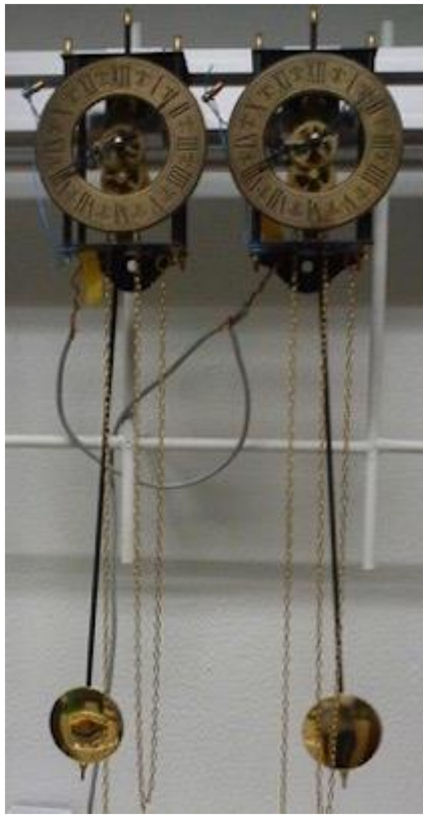
Historical background;

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*



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News

Synchronized swinging

Ancient pendulum conundrum solved.

John Whitfield

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.

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Huygens synchronization of two clocks

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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.

The synchronization between two periodic systems connected through some form of coupling is a recurrent, and still pertinent, problem in Nature, and in particular in Physics. During the 17th century Huygens, the inventor of the pendulum clock, observed phase or phase opposition coupling between two heavy pendulum clocks hanging either from a house beam and later from a board sitting on two chairs[1]. These two systems are inherently different in terms of the coupling process, and in consequence of the underlying model. The later case has been thoroughly studied[2-9] by considering momentum conservation in the clocks-beam system. The first case has been approached in theoretical works[10-13]. We present a mathematical model where the coupling is assumed to be attained through the exchange of impacts between the oscillators (clocks). This model presents the additional advantage of being independent of the physical nature of the oscillators, and thus can be used in other oscillator systems where synchronization and phase locking has been observed[14]. The model presented starts from the Andronov[15] model of the phase-space limit cycle of isolated pendulum clocks and assumes the exchange of single *impacts* (sound solitons, for this system) between the two clocks at a specific point of the limit cycle. Two coupling states are obtained, near phase and near phase opposition, the latter being stable. Our experimental data, obtained using a pair of similar pendulum clocks hanging from an aluminum rail fixed to a masonry wall, match the theoretical predictions and simulations.

Andronov model

The model for the isolated pendulum clock has been studied using models with viscous friction by physicists[1,3,5-9]. However, Russian mathematicians lead by Andronov published a work[15] where the stability of the model with dry friction is established (*Andronov clock*). The authors prove the existence and stability of the limit cycle.

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.

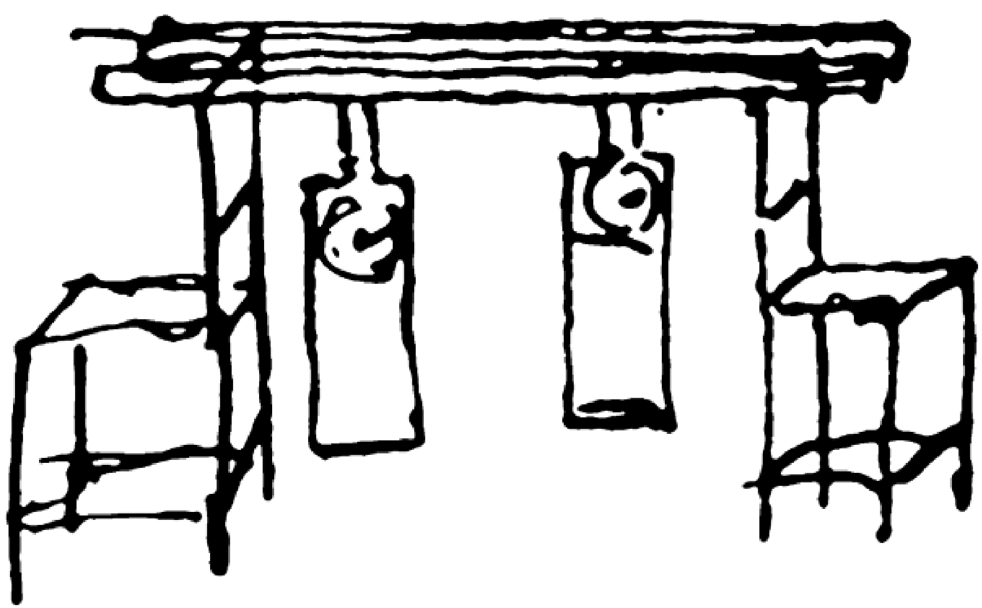
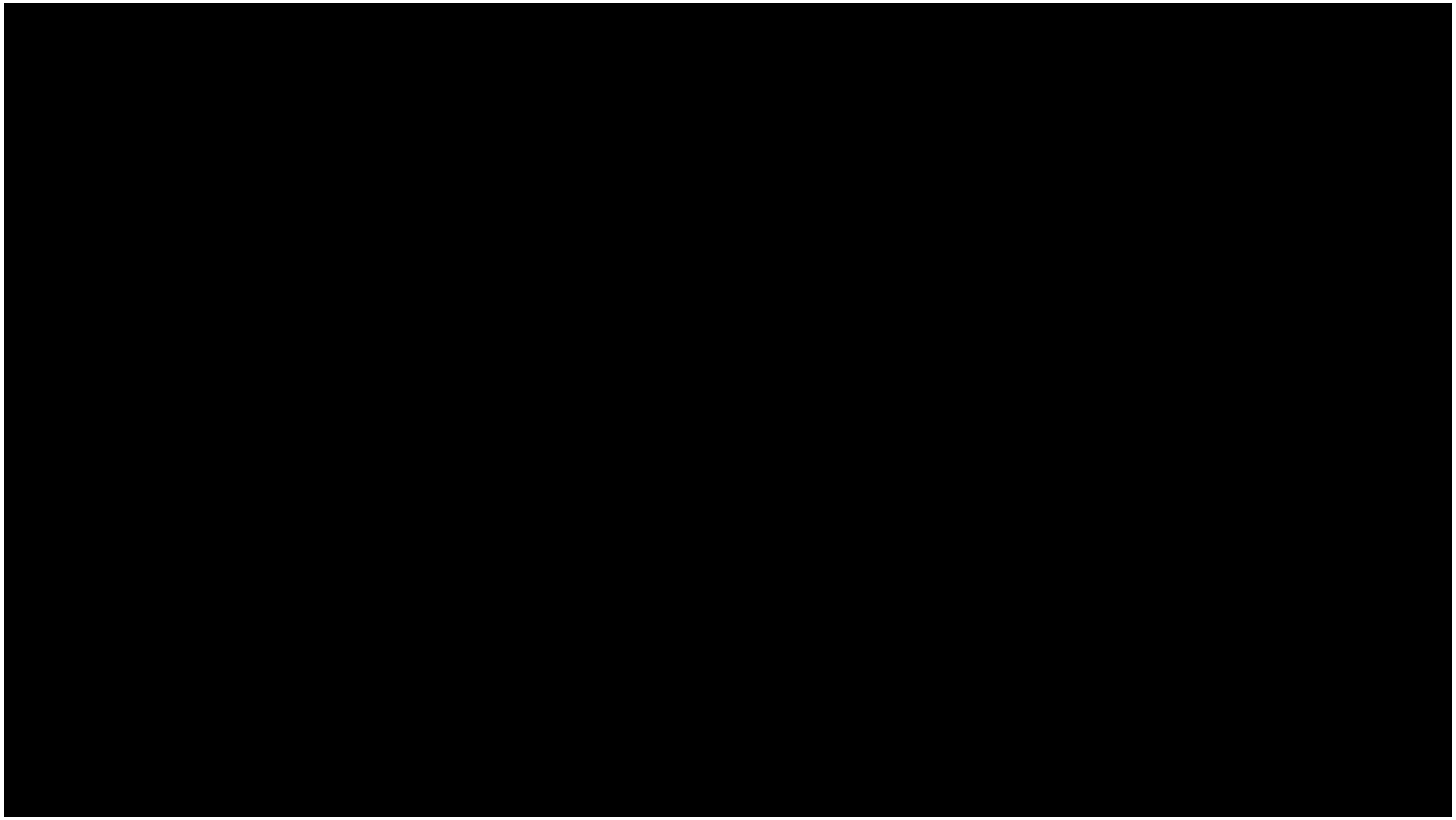


Figure 1.2. Original drawing of Christiaan Huygens illustrating his experiments with two pendulum clocks placed on a common support.

Oscillating metronomes – a demonstration



https://www.youtube.com/watch?v=bI2aYFv_978

It is everywhere…

- Mechanics
- Electronics
- Physics
- Chemistry
- Biology
- Economics,

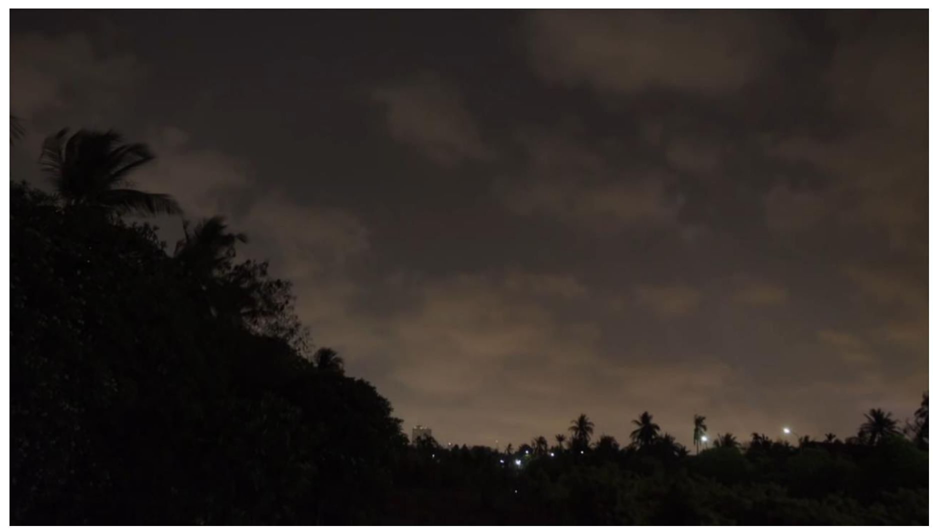
Figure 2.1 Examples of systems featuring collective synchronous motion: flocks of birds, coordinating aircrafts, orchestras, schools of fishes.

Until the 20th century, only some isolated observations appeared

Each element of the system coordinates its behaviour according to the behaviour of its neighbours and/or to an external force

- 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

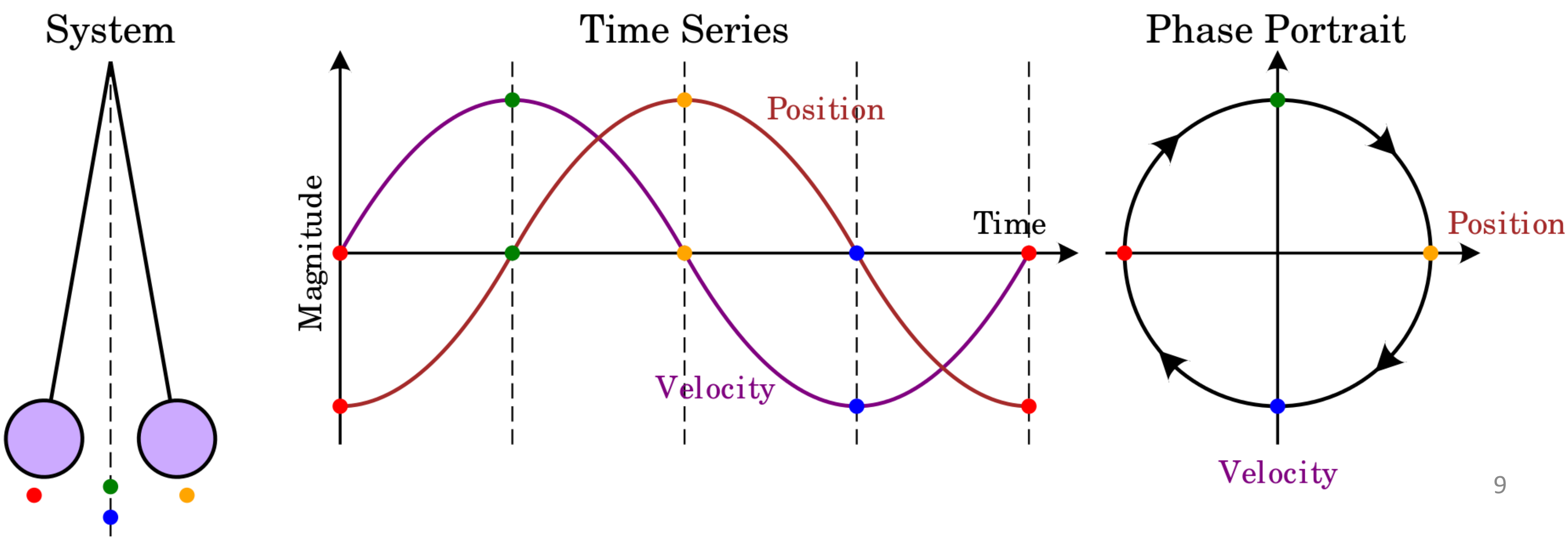
- Solution:

"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



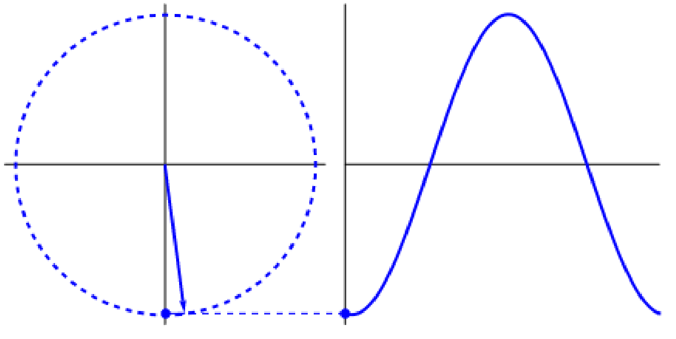
Phase oscillators

Def: A dynamical system with only one periodic dynamical variable ϑ

- ϑ is the ***phase*** of the oscillator
- fulfills $\dot{\vartheta} = F(\vartheta, t)$
- *F(θ, t)* is a real function that is 2π-periodic in ϑ
- Uniform phase oscillator: *F(θ, t)=ω*

  ω: angular frequency: a real constant

  The period of one oscillation is *T=2π/ω*



Types of coupling

Def: An *N*-dimensional system is called ***uncoupled***, if it can be decomposed in *k*<*N* independent dynamical subsystems with total dimension equal to *N*.

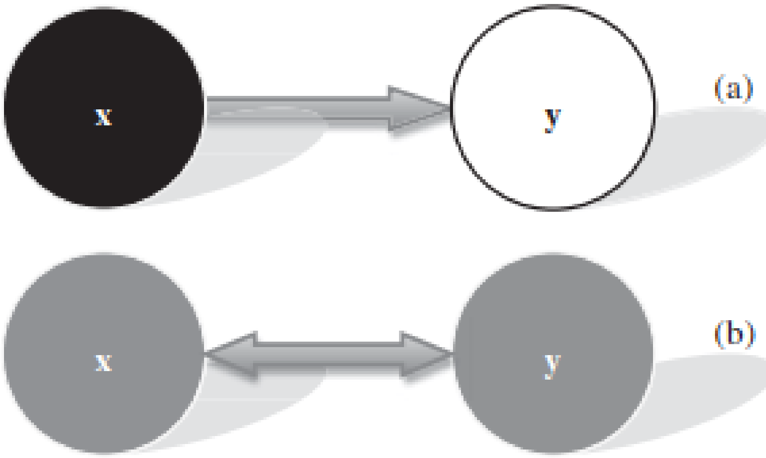
Simplest case: two oscillators (k=2):

$$\dot{\mathbf{x}} = \mathbf{F}(\mathbf{x}),$$
$$\dot{\mathbf{y}} = \mathbf{G}(\mathbf{y}),$$

Where $\mathbf{x} \in \mathbb{R}^n, \mathbf{y} \in \mathbb{R}^m$ and the total dimension is

$N = m + n$.

Coupling two oscillators



(a): unidirectional coupling

master-slave

(b): bidirectional coupling

Unidirectional coupling:

$$\dot{\mathbf{x}} = \mathbf{F}(\mathbf{x}),$$
$$\dot{\mathbf{y}} = \mathbf{G}(\mathbf{y}) + \mathbf{K}(\mathbf{x}, \mathbf{y})$$

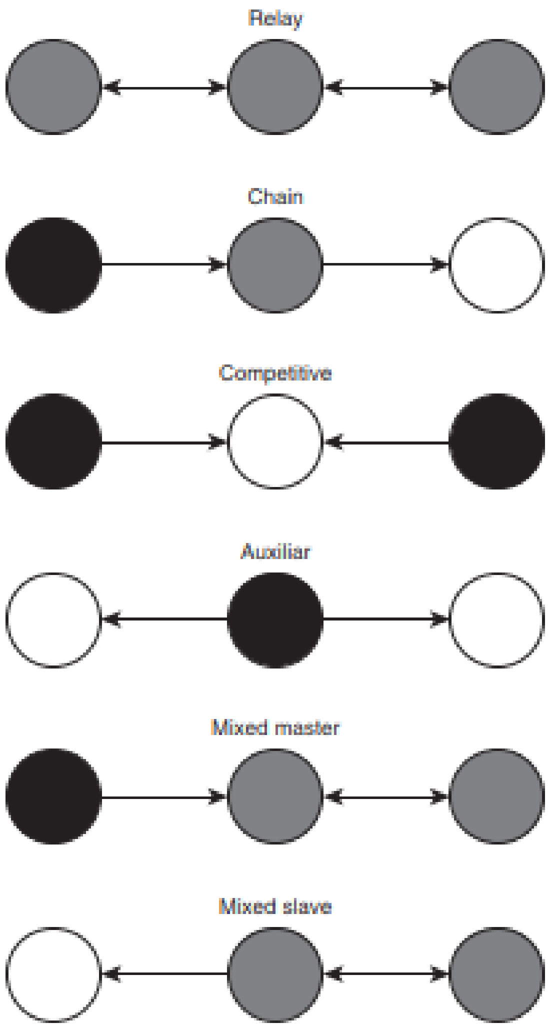
Where **K(x, y)** is a non-zero function of **x** and **y**.

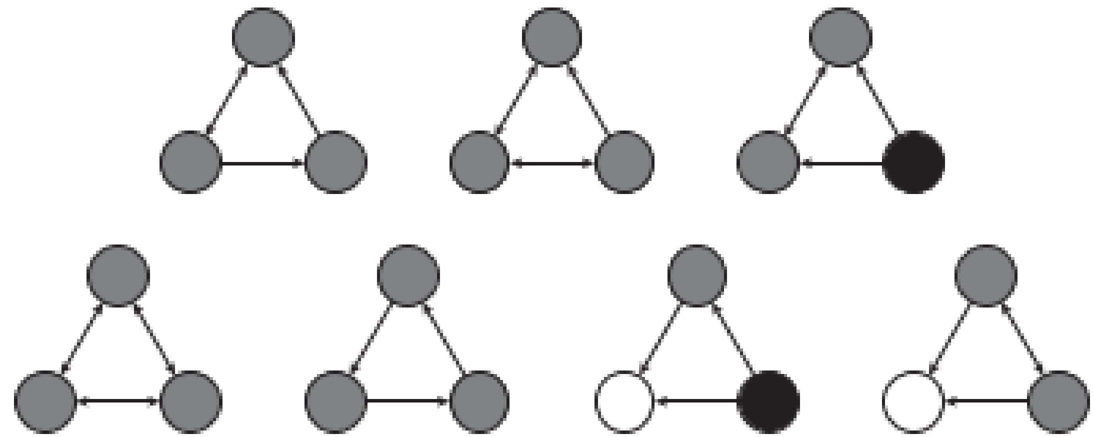
Bidirectional coupling:

$$\dot{\mathbf{x}} = \mathbf{F}(\mathbf{x}) + \mathbf{K}_1(\mathbf{y}, \mathbf{x})$$
$$\dot{\mathbf{y}} = \mathbf{G}(\mathbf{y}) + \mathbf{K}_2(\mathbf{x}, \mathbf{y})$$

Where $\mathbf{K_1(x, y)}$ and $\mathbf{K_2(x, y)}$ are non-zero functions of **x** and **y**. Symmetric: $\mathbf{K_1=K_2}$

Coupling three oscillators





Black: master system
White: slave system
Grey: systems that are mutually interacting

First models of biological oscillators

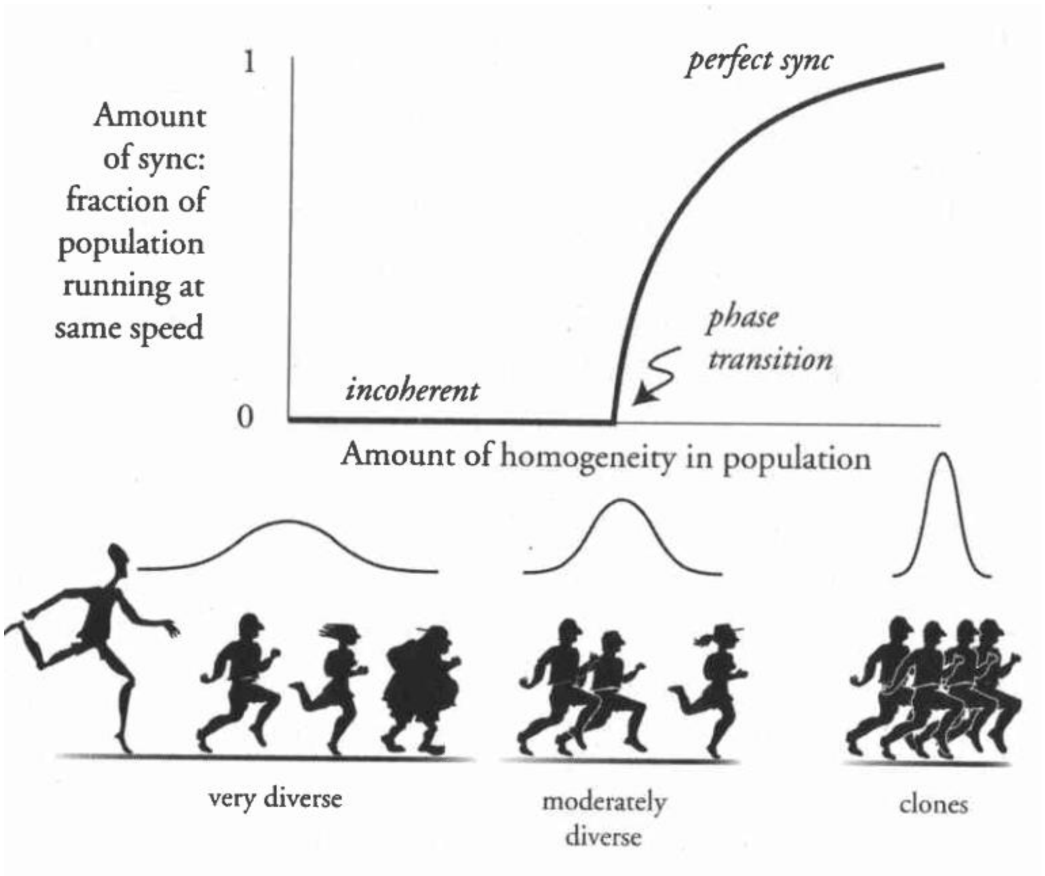
- Arthur Winfree, late 1960s
  - Ignored *all* biological differences and focused on the only common things: the ability to *send* and *receive signals*
  - Complication: both of these are often a function of phase
    - “Influence function” – what signal it sends
    - “Sensitivity function” – how an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

- 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
  - $\nu_i = \frac{1}{T_i}$: 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

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

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

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

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

- K : strength of the coupling
- If $\mathrm{K} > 0 \;\rightarrow \Gamma$ minimizes the phase difference

The Kuramoto model in mean field approximation

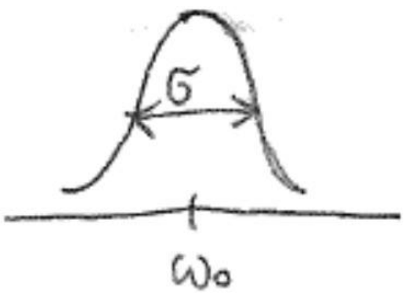
- The basic formula of the KM with MF approximation:

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

- 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:

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

- $\theta(t)$: 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.

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

Complex order param.   Real part $\frac{1}{N}N\left|\underbrace{e^{i\psi_j(t)}}_{=1}\right|$

- Z(t) is the real part of $z(t)$, → $Z = |z|$
- Z(t) is the *order parameter* with 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 ≈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.

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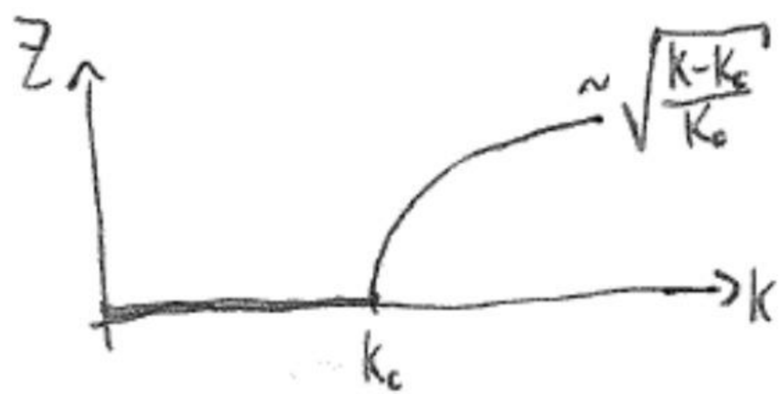

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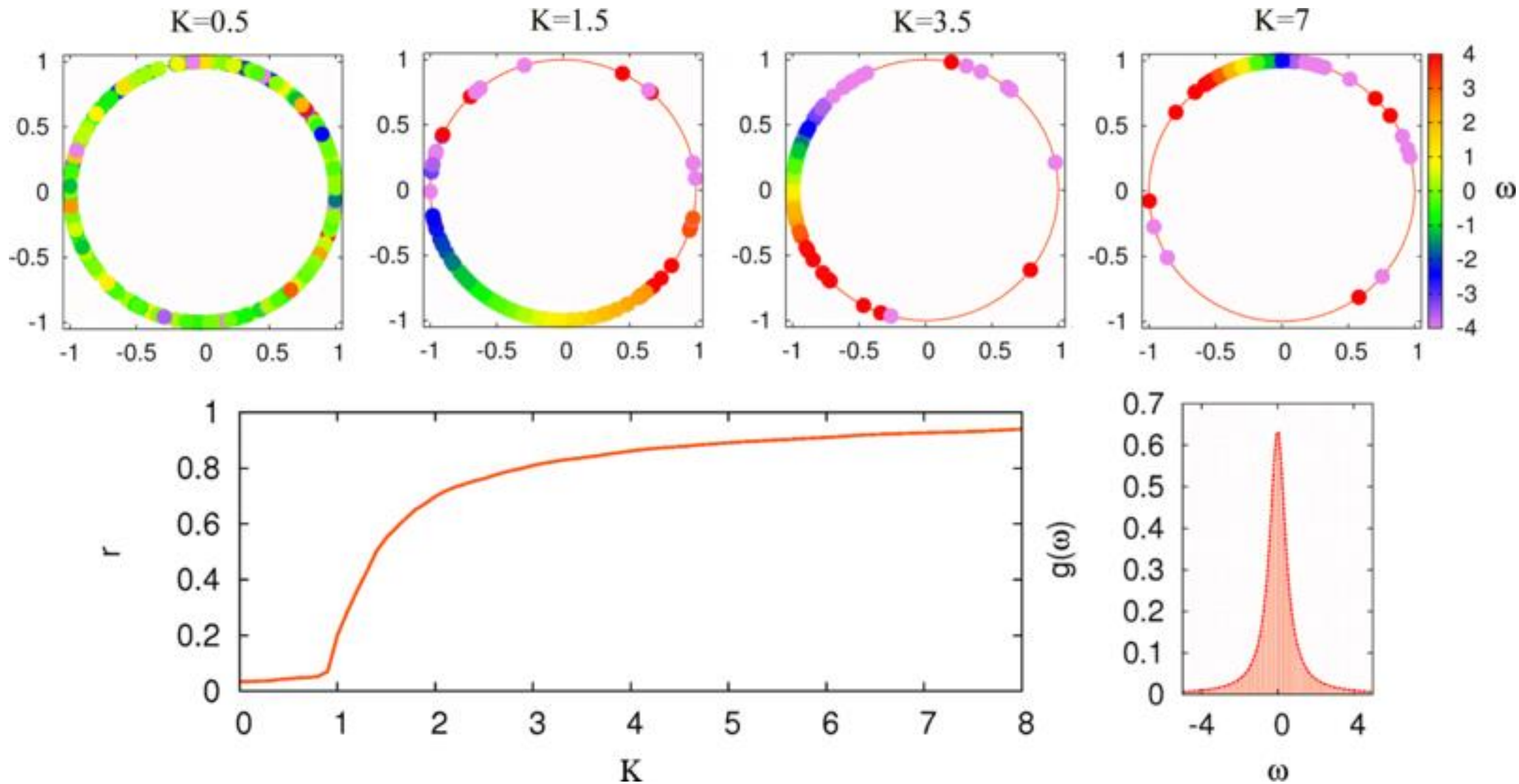
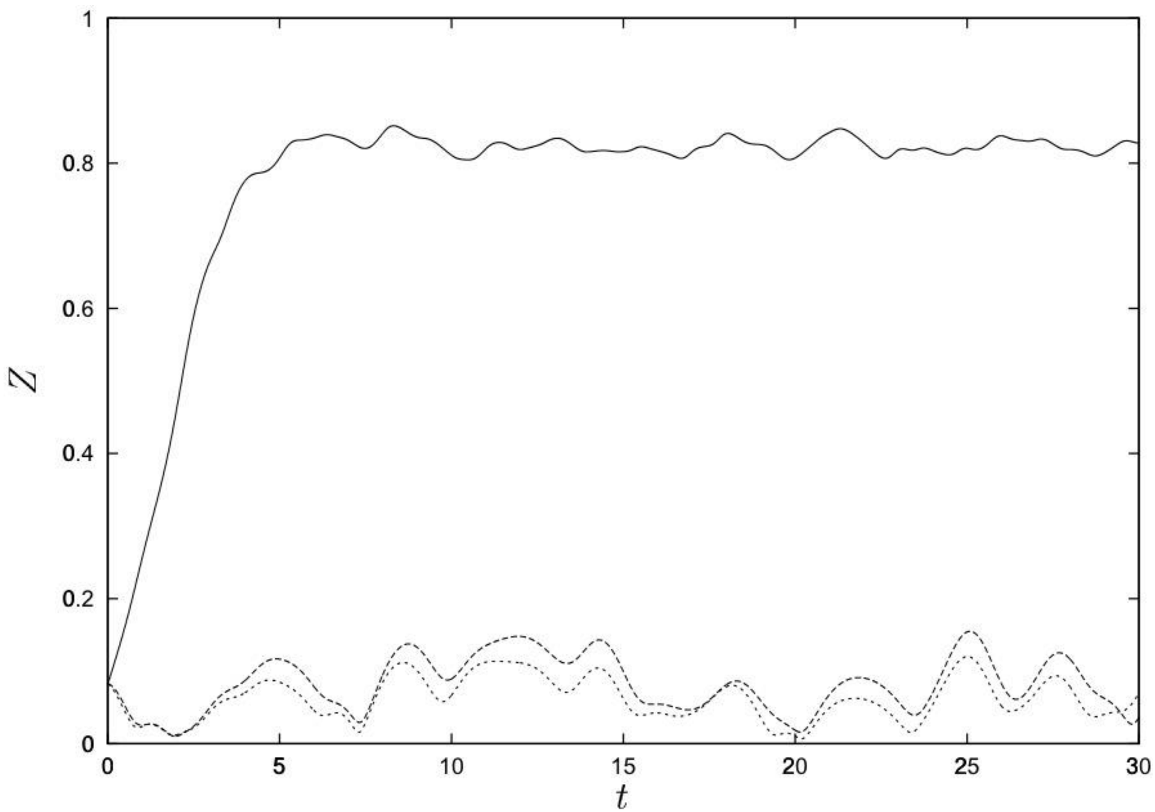


Synchronization in the classical Kuramoto model. Each panel on the top shows the collection of oscillators situated in the unit circle (when each oscillator *j* is represented as $e^{i\psi_j(t)}$).
The color of each oscillator represents its natural frequency. From left to right we observe how oscillators 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

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:

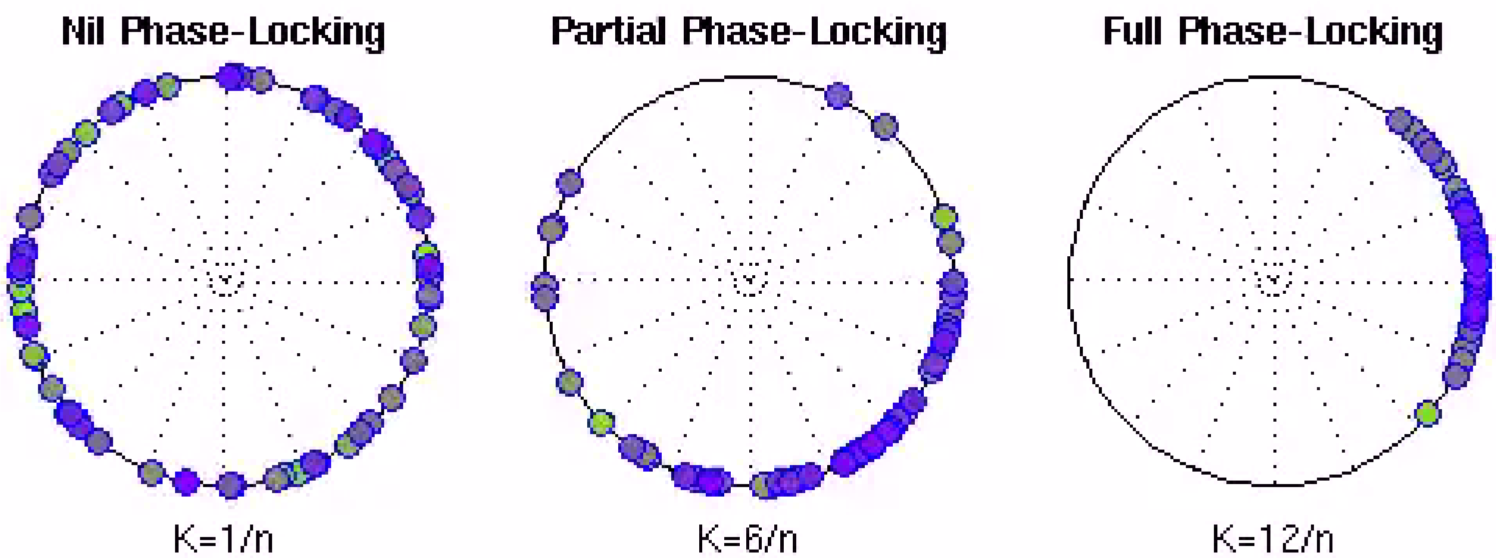
$$\frac{d\psi_i}{dt} = \omega_i + KZ\sin(\theta - \psi_i)$$

- 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 → the synchronization is not perfect → there are "drifting" oscillators)
  - **A**: The oscillators form a stationary distribution on the circle

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

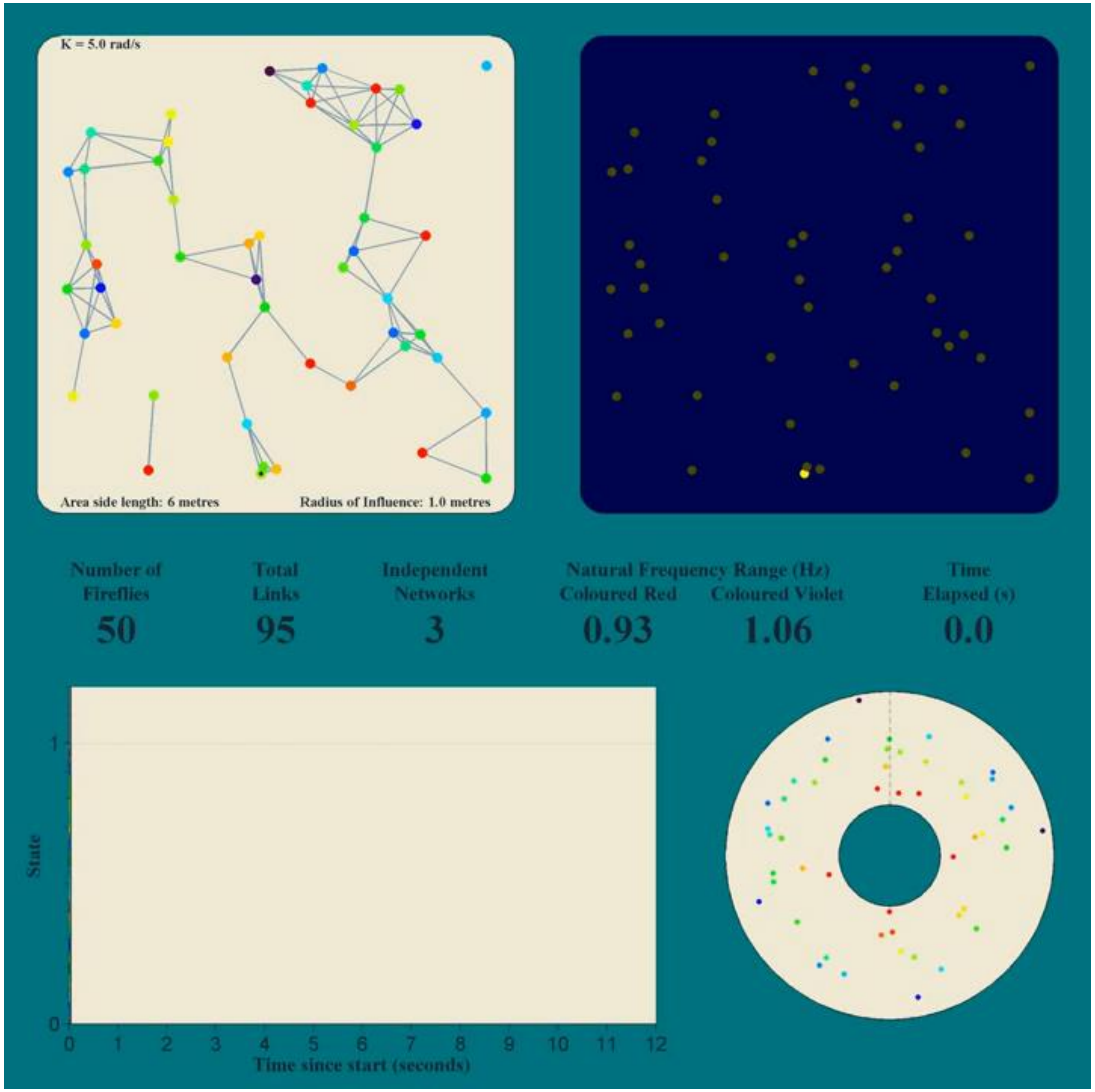
Phase-Coupled Oscillators



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.



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

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 analiticly
- 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 $\forall N$:

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

- If $\alpha \leq d$, then
  – If $N \to \infty$ 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)

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

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

- 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:

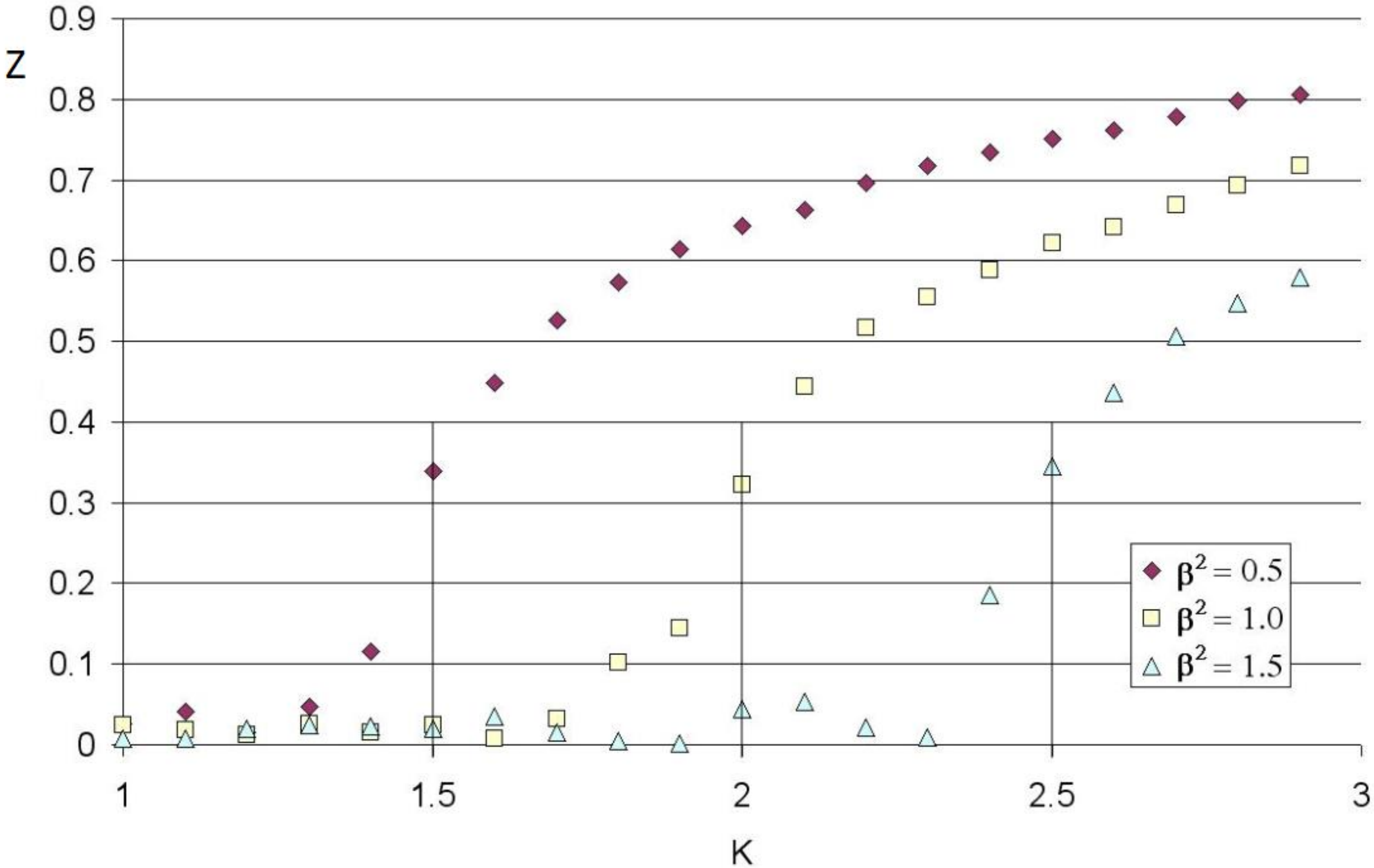
$$\frac{d\phi_i}{dt} = \omega_i + \frac{K}{N}\sum_{j=0}^{N-1} \sin\left(\phi_j - \phi_i\right) + \ \xi_i$$

- Or in other form:

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

- 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



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.

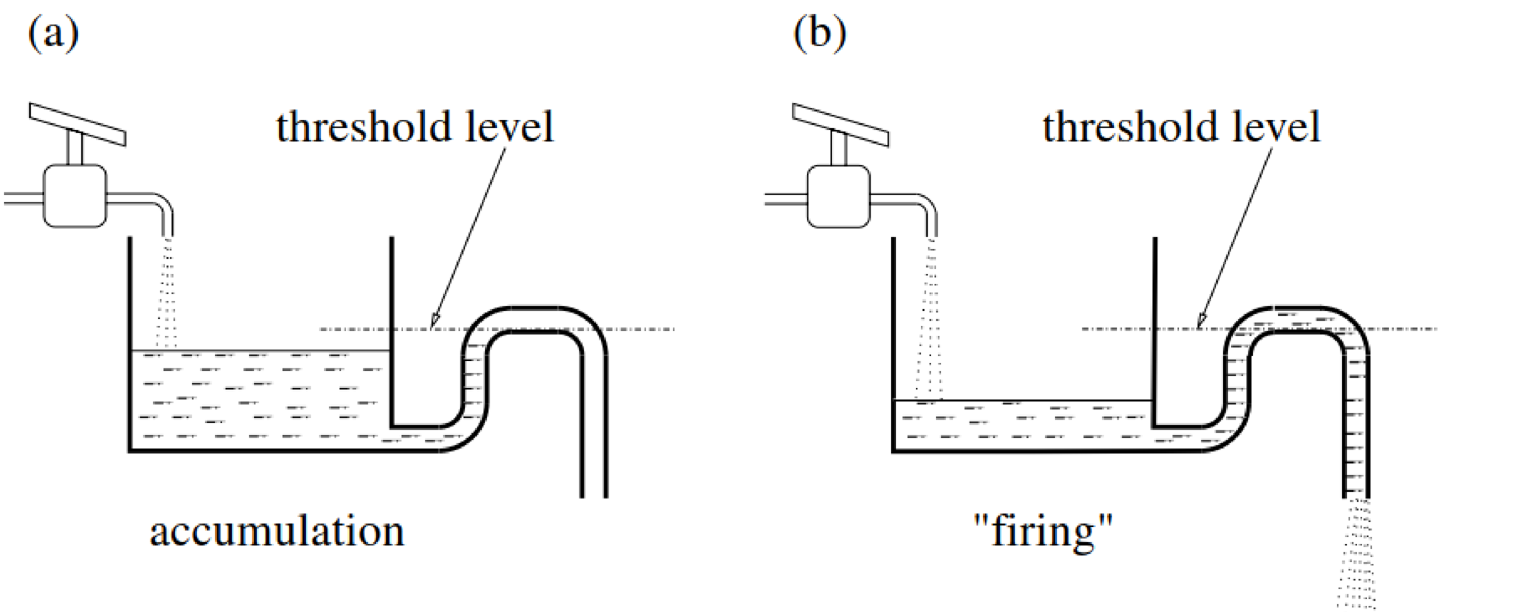
From: Bryan C. Daniels: Synchronization of Globally Coupled Nonlinear Oscillators: the Rich Behavior of the Kuramoto Model, Fig 4.2.

Relaxation oscillators

Basic feature: two time scales within each cycle

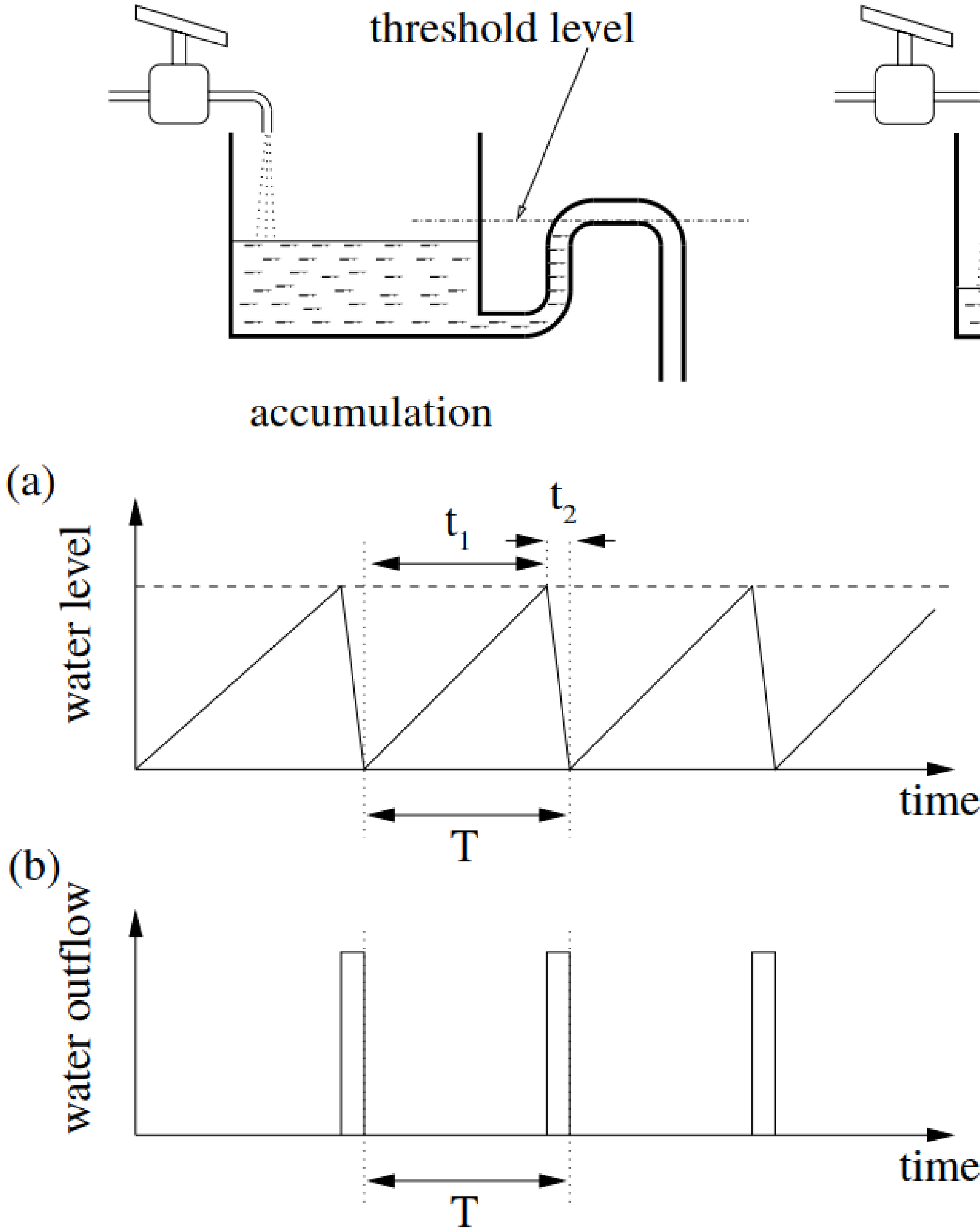
- A slow growth (linear or not)
- Fast resetting

→ *“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”.

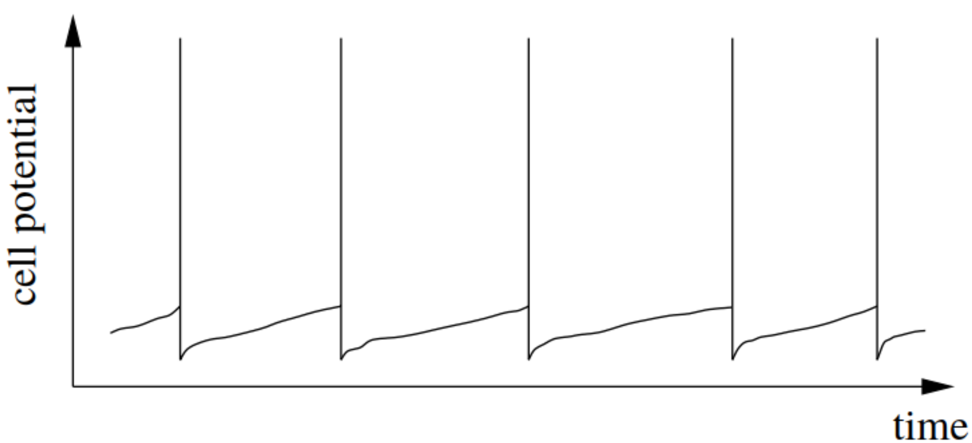


Time course of the mechanical integrate-and-fire (accumulate-and-fire) oscillator.
Water accumulates until it reaches the threshold level shown by a dashed line (a), then the water level is quickly reset to zero. The resetting corresponds to the pulse in the plot of the water outflow from the trap (b)

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.

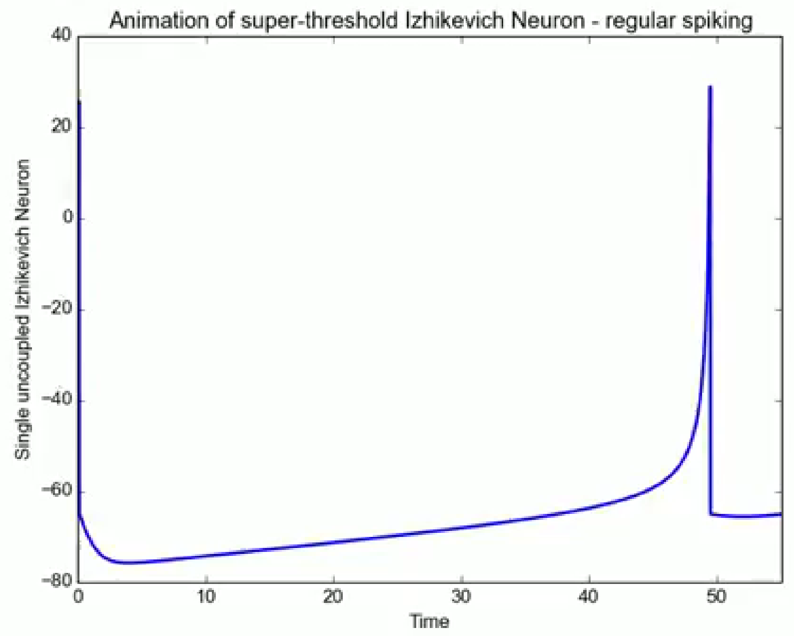
  A cycle
- When a constant current is injected into the cell, the action potentials are generated at a regular rate; slow variation of the current alters the firing rate of the neuron
- This is how sensor neurons work: the intensity of the stimulus is encoded by the firing rate.



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

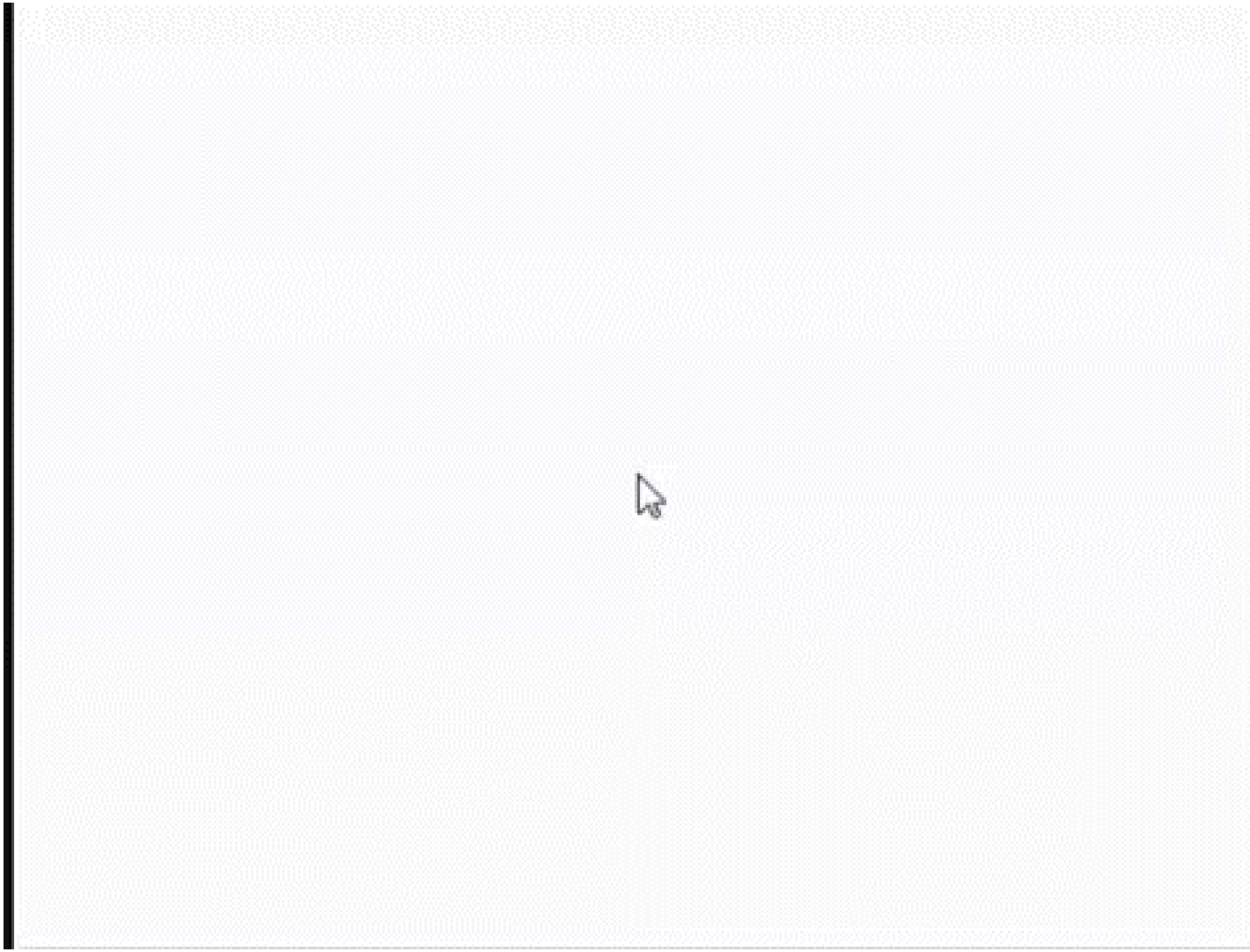
- A period of an IF
  - Monotonic increase up to a threshold value
  - When the threshold is reached, the oscillator relaxes to a basal level by firing a pulse to the other oscillators
  - A new period
- Synchronization is a central mechanism for information processing
  - Communication between brain 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=dsCItnAlh5k

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?

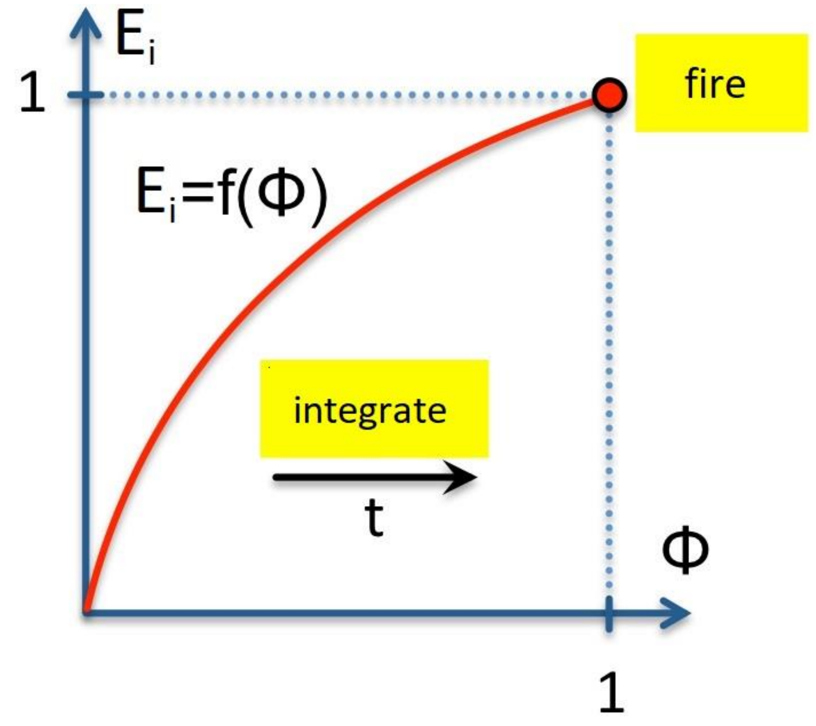
- What we will consider now:
  - Global all-to-all coupling
  - Identical oscillators
  - Convex, concave and linear
  - Without noise
  - Excitatory pulses
  - Without transmission delay and fall time

Describing one IF oscillator

- N IF oscillators, $O_i \quad (i = 1, \dots, N)$
- Each represented by a (real) state variable $E_i \in \left[0, E_i^{\ C}\right]$
- $E_i^{\ C}$: 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
$$f(0) = 0 \; and \; f(1) = 1$$

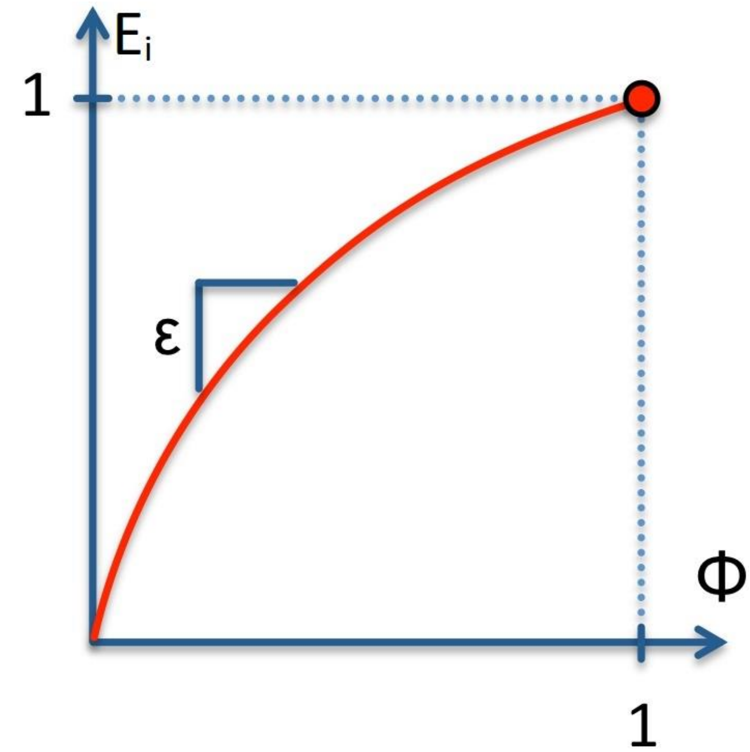
Assumption: the characteristic time for the relaxation is very short compared to the charging period; "instantaneous".

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 $E_j = 1$

  "phase advance model"
- 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)

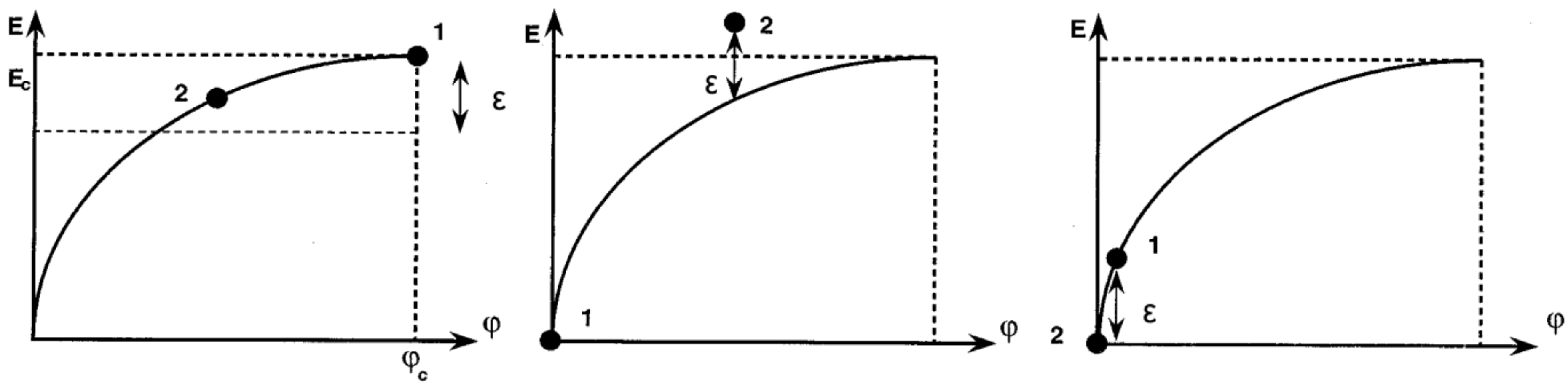


Excitatory → Increases E_j, and thus anticipating the firing. (this is the type we consider)

⇕

Inhibitory → 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.

From: Samuele Bottani, Synchronization of integrate and fire oscillators with global coupling, Physical Review E, Vol. 54, 1996, Fig 1

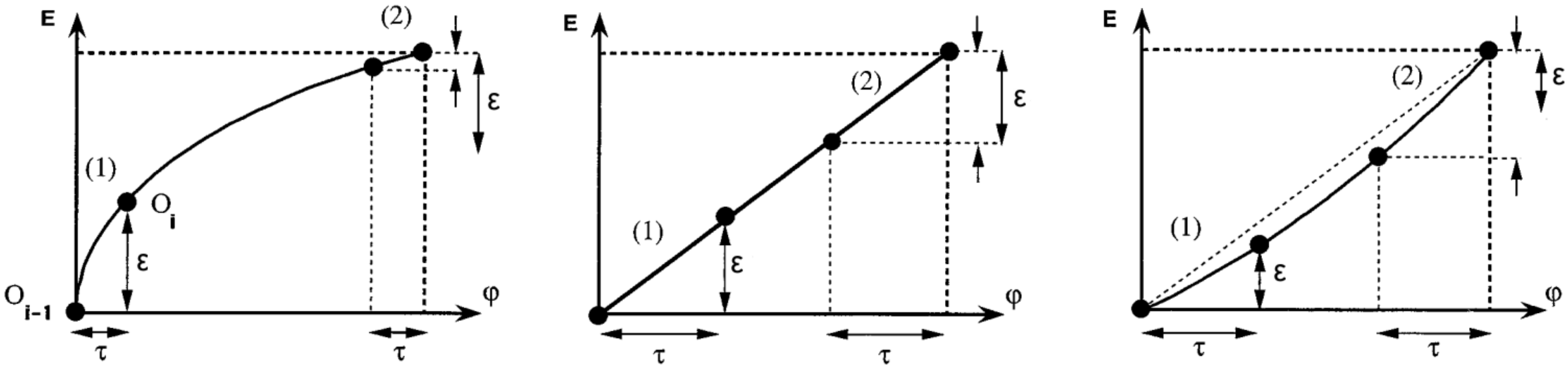
Avalanches and the absorption rule

- ***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.

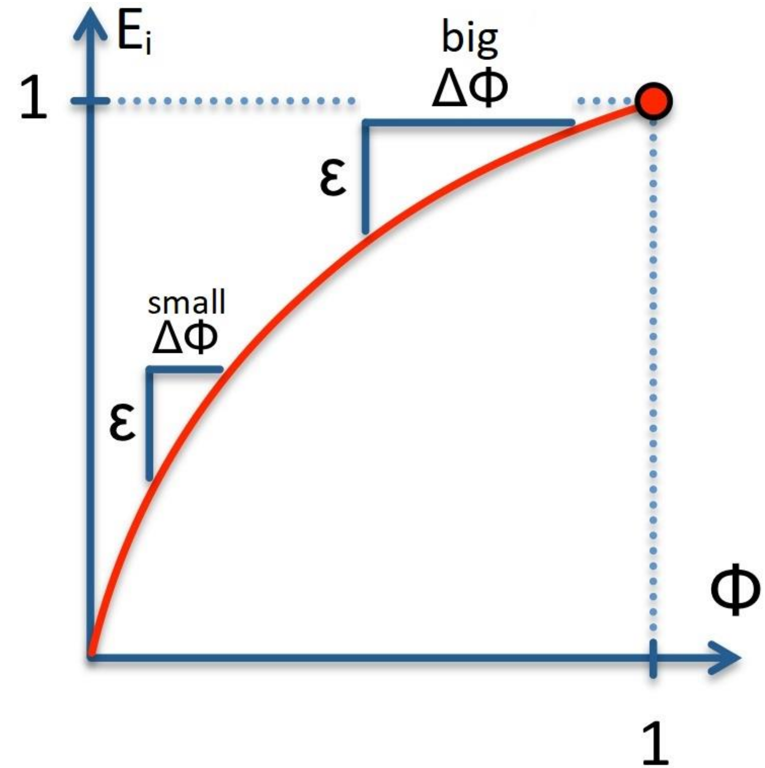
From: Samuele Bottani, Synchronization of integrate and fire oscillators with global coupling, Physical Review E, Vol. 54, 1996, Fig 2

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 completely[1]



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

- Convex
- Concave
- Linear

Synchronize, if *N* is big.[2]

[1]Mirollo and Strogatz, 1990
[2]Bottani, 1996