A Numerical Exploration of Synchronisation via the Kuramoto Model

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Abstract

The world is made up of complex systems: economic, biological, and ecological systems, amongst others, which exhibit a rich array of global dynamics, often typified as emergent properties of the localised interactions of a highly interconnected network of nodes.

Nodes of such systems typically have their own set of directives – cells or businesses for example operating within broader frameworks like organisms and economies. Clusters of nodes which share a set of directives repeat nearly identical tasks cyclically, oscillating between states at slightly different rates. There are many examples of systems whose global behaviours rely upon the clusters of oscillators syncing up spontaneously – without specific direction from any single 'leader'. Typical examples include pacemaker cells: which coordinate the heartbeat, neurones: which sync up their activity to perform a range of tasks, or even as a basis for social engagement; Pérez et al. (2017) demonstrated that conversational interactions between individuals can result in a phase locking of brain waves. Mathematicians have been keen to encode this phenomenon – termed 'synchronisation' - which occurs ubiquitously across natural systems of varying scale.

This project will provide an introduction to the Kuramoto model: a system of non-linear ODE's commonly used to model synchronisation. We will explore the history and derivation of the most general form of the model, followed by a numerical integration of the equation. Subsequent visual representations will then demonstrate how synchronisation emerges by increasing the level of pairwise node interdependency – a notion known as 'coupling strength'. We'll finish by exploring some of the adaptations made to the general form of the model, and how these relate to some recent application areas of significance.

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Introduction

In the literature, the Kuramoto model often appears without detailed explanation for its derivation. Any model is a generalisation of more complex phenomena, and the choices a modeller makes to restrict this complexity are not arbitrary; they're contextualised by a historical thread, woven through a myriad of previous works.

Prior to delving into the derivation of the Kuramoto model, we see a brief synopsis of this history and define some fundamental concepts on which the model relies, hopefully providing a gradual introduction for undergraduate mathematicians, without belabouring points made in other introductions.

Synchronisation

We can imagine starting two oscillators from two different points on a circle, then having them cycle through the circle at different rates. Suppose at some point in time, their frequencies drift toward one another until they're matching. Their positions will be different, but from any point thereon, they'll exhibit a constant phase difference.

We define phase as the proportion of the cycle travelled at time t. Synchronisation occurs when phases of the oscillators match.

Setting the scene

The first person to discover and then write about synchronisation was Christiaan Huygens in 1665. He noticed that two pendulum clocks (with slightly different initial phases) attached to the same wooden beam, would synchronise. The minute oscillations travelling through the beam had the effect of pairing the two clocks sufficiently to cause their pendulums to swing in phase.

Synchronisation phenomena was subsequently observed in many natural and man-made systems. Collective synchronization i.e. synchronisation of a large number of oscillators, was first studied mathematically by Norbert Wiener. *Unfortunately, Wiener's mathematical approach based on Fourier integrals turned out to be a dead end* (Steven H. Strogatz, 2000).

The approach others have taken since depends on how oscillators themselves are characterised, so we will briefly observe these different characterisations.

Relaxation oscillators

One characterisation is that of the relaxation oscillator, an oscillator whose behaviour over time evolves steadily until a certain threshold is reached. At this point some activity is performed (perhaps a pulse being sent across a synapse after a building of action-potential), the oscillator then returns to its initial state and the cycle continues. Clearly this periodicity isn't represented by a smooth waveform and instead exhibits a jagged profile.



Transient analysis of a comparator-based relaxation oscillator. By Krishnavedala, CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=15442360

The first equation to describe the dynamics of a relaxation oscillator was developed in 1927 by Balthasar Van der Pol, a Dutch physicist who utilised the equation to model the human heart via three coupled "Van der Pol oscillators".

Self-sustaining oscillators

Some objects oscillate simply because an external periodic force acts upon them; they do not maintain their own periodic motion internally. Other oscillators are described as 'self-sustaining'; their periodicity is self-generated in the absence of a periodic external power supply. The pendulum clock is an example of a self-sustained oscillator, as noted by Binder, M.D., Hirokawa N., Windhorst U (2009), as are *many important and familiar natural phenomena, such as the heartbeat, the firing of neurons, ocean waves, and the pulsation of variable stars* (Jenkins , 2013).

An important property of self-sustaining oscillators is that since their motion is self-governed, if they're perturbed slightly, they eventually return to their regular motion. As a result, their trajectories can be modelled via stable limit cycles.

Limit cycles

Limit cycles are isolated, closed trajectories of *non-linear* dynamical systems, and are not to be confused with centres, which are periodic trajectories of *linear* dynamical systems. For limit cycles, if we start from a point outside of the cycle, there are no other periodic cycles to be found nearby and its trajectory will eventually converge to the cycle.

Arthur Winfree, an engineering physicist turned biologist, was the first to attempt to model synchronisation in a *large* network of biological oscillators, each represented as weakly coupled limit-cycle oscillators.

Project scope

In this project we will build our intuition around the development of the Kuramoto model, then solve the model via numerical integration using MATLAB, applying it to a set of 500 oscillators. Solving the ODE generates phases for the oscillators which we then plot as a function of time. To take this further, we introduce an equation for an order parameter, which quantifies the similarity of phases at a given time for an assumed coupling parameter V. We will vary this coupling parameter, demonstrating that at a certain critical value, synchronisation will occur.

The Kuramoto Model

Since the Kuramoto model is based on many of the same assumptions as the Winfree model, we'll start to build our intuition for the model here.

Winfree oscillators

Suppose there are n interacting self-sustained limit-cycle oscillators in a network. The first assumption we make is that they're nearly identical. We expect the intrinsic frequencies of the oscillators to be sufficiently similar so that they're represented within the same probability distribution, in which we have expected (mean) frequencies.

We also know that the oscillators are affected by one another; they're 'coupled' *through metabolic, bioluminescent, electrical, mechanical or other channels* (Winfree, A. T, 1967). In the absence of this coupling, each oscillator is left to operate independently and therefore maintains its own frequency, allowing no synchronisation to occur.

In modelling the evolution of individual oscillators within such a system, we start with this intrinsic frequency ω_i and then take into account the influence of all the other oscillators. We avoid further complication by ignoring outside interference – that is, anything outside of the network of oscillators which may also influence their frequencies. This forms an ODE in an n-dimensional vector space.

We previously mentioned a property of stable limit cycles: that trajectories originating within a neighbourhood of the limit cycle will spiral into it. We won't formally define how we would find this neighbourhood, but it suffices to say that trajectories originating from outside of it may not converge to the limit cycle. This could occur for an oscillator if the influences of other oscillators cause a sufficiently strong perturbation. In order to avoid this, Winfree required that no oscillator could be significantly affected by the total influence of the others, they must be coupled 'weakly'⁽¹⁾ so as not to take them away from the limit cycle.

Now that we've ensured the oscillators traverse the same limit cycle regardless of perturbation, albeit at differing frequencies, we have reduced the problem from consideration of dynamics in an N-dimensional vector field, to description of pertinent inter-relations among functions of a single scalar variable, namely phase in the cycle (Winfree, A. T. 1967). This just means that since they're traversing the same cycle, we'll always know the position simply by observing a single parameter: the phase.

Winfree defined an 'influence function' X, which output the level of influence for an oscillator depending on its phase. The sum of these (weak) influences for all oscillators in the network is denoted by 'S' for 'stimulus'.

$$S = \sum_j X(\phi_j)$$

He also defined a 'sensitivity function' Z, as follows:

$$Z(\phi) = \lim_{s \to 0} \frac{\Delta f}{S}$$

This represents the change in frequency of an oscillator when perturbed by an arbitrarily small stimulus. It's also dependent on phase, so this tells us that the sensitivity of an oscillator depends on where it is within its oscillation period.

Together, the stimulus and sensitivity function represent a 'mean-field'. The equation we arrive at is as follows:

$$\frac{d\theta_i}{dt} = \omega_i + \left(\sum_j X(\phi_j)\right) Z(\phi_i), \quad i = 1, \dots, N.$$

Using this model, Winfree derived the following property of limit cycle oscillators; under certain threshold conditions relating to both the strength of the stimulus and the sensitivity function, oscillators will synchronise their frequencies to that of a periodic stimulus.

(1) Winfree restricted his attention to weak interactions in which Z and X were both less than 10% of the size of the average frequency of an oscillator.

Deriving the Kuramoto model

Whilst Winfree demonstrated synchronisation numerically, his model was analytically difficult to solve. Kuramoto, taking the baton from Winfree's approach, developed a solvable model in 1975.

Kuramoto was primarily motivated by a desire to model synchronisation behaviour within chemical reactiondiffusion systems, though he reflected on the broader applicability of his model to other synergetic natural processes.

Stuart Landau oscillators

A system which is dissipative i.e., a system that is thermodynamically open, in that it exchanges information with its environment, is typically dependent on a number of parameters. Exploring how the system behaves as a result of small variations in the parameter values is known as perturbation theory. This can greatly reduce the complexity of modelling a real-world system, as its behaviour is approximated via a more succinct dynamical equation. Dissipative systems very close to a Hopf bifurcation can - through perturbation analysis - be represented via the Stuart-Landau equation.

Kuramoto derived a more general form of the Stuart-Landau equation, called the Ginzburg-Landau equation, in order to overcome limitations of the Stuart-Landau equation in representing systems of larger size:

$$\frac{dQ}{dt} = (\omega i + \alpha)Q - \beta |Q|^2 Q$$

Where α , $\beta > 0$, and Q is a complex variable signifying disturbance, representable via Euler's formula in its exponential form as Q(K, θ) =K $e^{i\theta}$.

Calculating partial derivatives, we have:

$$\frac{\partial Q}{\partial K} = e^{i\theta} \qquad \qquad \frac{\partial Q}{\partial \theta} = Kie^{i\theta}$$

$$\frac{\partial Q}{\partial t} = \frac{\partial Q}{\partial K}\frac{\partial K}{\partial t} + \frac{\partial Q}{\partial \theta}\frac{\partial \theta}{\partial t} = e^{i\theta}\frac{\partial K}{\partial t} + Kie^{i\theta}\frac{\partial \theta}{\partial t} = (\omega i + \alpha)Ke^{i\theta} - \beta|K|^2Ke^{i\theta}$$

Rearranging and simplifying, we have:

$$\frac{\partial K}{\partial t} + Ki \frac{\partial \theta}{\partial t} = \omega i \mathbf{K} + (\alpha - \beta |K|^2) \mathbf{K}$$

Equating real and imaginary parts:

$$\frac{\partial K}{\partial t} = (\alpha - \beta |K|^2) K \qquad \frac{\partial \theta}{\partial t} = \omega$$

Looking at Q in terms of polar coordinates, we have $Q = K(isin\theta + cos\theta)$

If we imagine this as a traversal of a (limit) cycle of radius K, we have a cycle where $\theta = \omega t$ varies in time.



This requires us to fix K in time, so we look for solutions to $\frac{dK}{dt} = 0$. This occurs when $\alpha - \beta K^2 = 0$ i.e. radius K = $\sqrt{\frac{\alpha}{\beta}}$

A system of interacting oscillators

Suppose we have N interacting Ginzburg-Landau oscillators of varying frequencies. Each oscillator can be represented by the following equation:

$$\frac{\partial Q_i}{\partial t} = (i\omega + \alpha)Q_i + \sum_{j \neq i} v_{ij}Q_j - \beta |Q_i|^2 Q_i$$

This takes into account the effects the other N-1 oscillators have on oscillator i.

Kuramoto used a 'mean-field' assumption, similar to Winfree, to simplify the model somewhat:

Vij = $\frac{V}{N}$ for all i,j

Repeating the same steps as in the individual oscillator case, after equating real and imaginary parts we have:

$$\frac{\partial K}{\partial t} = (\alpha - \beta |K|^2) K + \frac{V}{N} \sum_{j \neq i} \cos(\theta_j - \theta_i) \qquad \qquad \frac{\partial \theta_i}{\partial t} = \omega_i + \frac{V}{N} \sum_{j \neq i} \sin(\theta_j - \theta_i)$$

The right-hand side equation is the Kuramoto model. Similar to Winfree's model, the model is simplified since each oscillator is approximately specified by its phase value. *Thus the dynamics of our system of N discrete oscillators may be reduced to N coupled ordinary differential equations for N phase variables* (Kuramoto, 1983).

The order parameter

Suppose we plot the initial N oscillators on a circle. At various times, we want to have some way of determining the level of coherence i.e, how clustered together their phases are.

Kuramoto defined an order parameter on this basis, distributing oscillators on the unit circle so that their positions were represented by unit vectors. The sum of these vectors, divided by the number of oscillators N, is how he defined the order parameter.

$$r(t)e^{i\varphi} = \frac{1}{N}\sum_{j}e^{i\theta(t)_{j}}$$

The order parameter is therefore a complex variable, dependent on time, which we can view as a vector pointing from the origin of the circle, with angle φ (the average of the phases of the oscillators).

The magnitude of the vector quantifies the level of coherence, differing depending on how close the oscillators are to one another. For example, if the oscillators have identical phase, then the above formula reduces to:

$$\frac{1}{N} * N e^{i\theta(t)} = e^{i\theta(t)}$$

The magnitude $|e^{i\theta(t)}|$ is 1. This is the value associated with complete coherence. Alternatively, if the oscillators are placed as far from one another as possible (distributed uniformly on the unit circle) then by symmetry of sine and cosine, for uniform phases, the equation cancels to 0.

$$\frac{1}{N}\sum_{j}e^{i\theta(t)_{j}} = \frac{1}{N}\sum_{j}isin\theta(t)_{j} + cos\theta(t)_{j} = \frac{1}{N}*0 = 0$$

The critical value of the coupling parameter V

Kuramoto derived a critical coupling value at which synchronisation could be analytically proven to occur, defined as the following:

$$V_c = \frac{2}{\pi g(0)}$$

Where g is the probability distribution function used to draw intrinsic frequencies ω_i , required by Kuramoto to be symmetric and unimodal (Winfree did attempt to use bimodal distributions for his numerical analysis, but found

that this resulted in two synchronised clusters, bimodal distributions have subsequently been studied in adapted forms of the general Kuramoto model).

We have opted to use the standard normal distribution, so g in this case is given by:

$$g(x) = \frac{1}{\sqrt{2\pi}}e^{-\frac{x^2}{2}}$$

Hence $g(0) \approx 0.399$

Thus, our critical value is $V_c \approx 1.6$

We will therefore focus our attention numerically on coupling values V = 0, 1, 1.5, 2, 3.

Numerical integration

We first define the ODE as a function within MATLAB. We initially specify the coupling parameter V and number of oscillators N as local variables, then iterate over the oscillators to build an ODE vector for a single time step. We specify the time interval we're iterating over, and we create a vector of initial conditions by first drawing 500 random values between 0 and 1, then multiplying by 2*pi (the perimeter of the unit circle). This gives us a random variety of different initial phases at t = 0.

```
function dYdt = kuramoto_experiment_2(~,X,Y)
V = 2;
N = 500;
for p = 1:N
    for s = 1:N
        X(p) = X(p) + (V/N)*sin(Y(s) - Y(p));
    end
end
dYdt = X;
end
```

For simplicity we choose to draw our intrinsic frequencies randomly from the standard normal distribution. Finally, we find an approximation for the evolution of phases, via MATLAB's built in ODE solver: ode45.

Visual demonstration of synchronisation

```
t = [0 500]
y0 = 2*pi*rand(1,500)
X = randn(500,1)
A = 0
for n=1:500
A = A + exp(i*Ysol(:,n))
end
A = (1/500)*abs(A)
plot(tSol,A)
```

For varying coupling strengths (V = 0, 1, 1.5, 2, 3). We calculate the magnitude of the coherence parameter, then plot this as a function of time.

From figure 1 we see that after approximately T = 5 time steps, for a coupling value V = 3, the magnitude of the coherence parameter nears 1, indicating synchronisation. To a lesser but still pronounced extent, after approximately T = 10 time steps, for a coupling value V = 2, the magnitude of the coherence parameter oscillates around 0.7. This is approximately in line with our earlier observation of a critical value existing at $V_c = 1.6$.



Figure 1: A graph showing the evolution of coherence for different coupling strengths.

We would therefore expect to see a clustering of phases at V = 2, which we visualise by first generating the unit circle, then plotting phases at different times.

```
for n = 1:500
r = 1;
xc = 0;
yc = 0;
theta = linspace(0,2*pi);
x = r*cos(theta) + xc;
y = r*sin(theta) + yc;
plot(x,y)
axis equal
end
hold on
scatter(cos(y0),sin(y0),'*')
```



Figure 2: A plot of phases on the unit circle at different times.

We now take a closer look at how phases evolve over time. For a value at which synchronisation is clearly occurring (V=3), we see in figure 3 that phases are randomly distributed initially, with a pattern beginning to emerge after only a few time steps.

Then, zooming out to encompass the full extent of time steps, we can see in figure 4 that the phases traverse the unit circle in tandem, resetting periodically.



Figure 3 and 4: Graphs showing the evolution of phase for 500 oscillators, with coupling strength V = 3.

Further exploration

The simplicity of the model, combined with its broad range of applications has meant it has become one of the primary tools for studying synchronisation, and has seen a number of different adaptations since its conception. We'll briefly explore some of these adaptations and then some areas of recent (and significant) application.

The presence of noise

Synchronisation is known to be affected by noise i.e. random deviations inherent within natural systems, like thermal fluctuations. Noise can be added to the Kuramoto model as below, by adding a value drawn randomly from a (typically Gaussian) distribution. This can add to the plausibility of the model for representing real systems:

$$\frac{\partial \theta_i}{\partial t} = \omega_i + \frac{V}{N} \sum_{i \neq i} \sin(\theta_i - \theta_i) + \eta_i(t)$$

Complex Networks and the Kuramoto model

Complex networks are graphs which represent complex systems – or more specifically, the nodes within complex systems and their interactions. Synchronisation and Complex Networks are two interwoven topics of study. A paper in the late 90s - arguably one of the founding papers of the field of Complex Networks - written by Duncan J. Watts and Steven Strogatz, consisted of *the idea of including shortcuts between oscillators connected as a regular graph to analyse how crickets synchronize their chirps* (Rodrigues et al, 2016). Since then, a great deal of emphasis has been placed on determining how network structure influences synchronization.

Initially, the model was studied in complete graphs – simple undirected graphs, where every pair of distinct nodes are connected by a unique link. This is known as all-to-all coupling, and isn't always realistic in modelling real complex systems, where connections between nodes exist in some instances and not others.

The Kuramoto model is adapted to this perspective as follows:

$$\frac{\partial \theta_i}{\partial t} = \omega_i + \sum_{i \neq i} \gamma_{ij} A_{ij} \sin \left(\theta_j - \theta_i \right)$$

Where A_{ij} is the (i,j) entry to the adjacency matrix of a complex network, corresponding to 1 in the presence of a link between nodes, and 0 otherwise. γ_{ij} is the coupling strength between nodes i and j. In a fully connected graph, the approximation $\gamma_{ij} = \gamma$ is used.



Figure 5: Pictorial and matrix representation of different network models. Taken from 'Generalising the Kuramoto model for the study of neuronal synchronisation in the brain' by D. Cumin, C. and P. Unsworth (2007).

If we abandon all to all coupling then we allow for clusters of nodes to occur, or 'hub' nodes which have more influence than others. There is therefore significant attention paid to how the degree distribution of nodes affects synchronisation. For example, numerical analysis has found that *networks with a high occurrence of triangles reach lower levels of synchronization in comparison with networks with the same degree distribution at the same coupling strength* (Rodrigues et al, 2016). Other adaptations allow for time-delayed coupling and evolving networks, in which nodes join the network at different times.

In recent years, many attempts have been made to expand the analysis of the Kuramoto model to different classes of network models, allowing the topological properties of different systems of oscillators to be explored.

Recent areas of application

We observe two examples of important application areas in recent years: power-grid networks and cortical networks.

Power-grid networks

Power grid networks consist of a network of generators, which convert sources of energy into electricity, and consumers/machines which do the opposite. There are therefore two kinds of dissipative oscillators, whose overall set of intrinsic frequencies are best modelled as originating from a bimodal distribution.

Continuation is an important component of power-grid networks i.e., for energy to flow seamlessly throughout. Synchronisation of oscillators is therefore important. Otherwise, areas of the network may become overloaded or vulnerable to small fluctuations. Dramatic events like power outages may occur if the system transitions to incoherence.

It's therefore of interest to develop a robust model for the synchronisation of such oscillators, and estimation of the coupling parameter V at which synchronisation occurs. This was achieved by Filatrella, G., Nielsen, A. and Pedersen, N in 2008, in which a second order Kuramoto model was derived, as below:

$$\frac{\partial^2 \theta_i}{\partial t^2} = \omega_i - a \frac{\partial \theta_i}{\partial t} + K \sum_{j \neq i} A_{ji} \sin \left(\theta_j - \theta_i \right)$$

 A_{ji} are entries of an adjacency matrix **A** which convey the existence of transmission lines between electrical generators.

Cortical Networks

Prior to the Kuramoto model's development, in the late 1950's, Norbert Wiener hypothesised that synchronisation of brain waves was a result of tempering effects between neuronal oscillators. Neuronal synchronisation has been observed extensively experimentally in subsequent years and numerical simulations are increasingly deployed to study the phenomena.

This is one example where the model must be adapted to accommodate properties of cortical connectivity relating to their spatial distribution. For example, a model devised by Breakspear, M, Stewart, H and Daffertshofer, A in 2010, integrated time delays to represent the distance between dense (fully connected) neurons within the cortical sheet:

$$\frac{\partial \theta_i}{\partial t} = \omega_i + \frac{V}{N} \sum_{j \neq i} \sin \left(\theta_j - \theta_i - a_{ij} \right)$$

where a_{ii} is a spatially dependent parameter representing time delay.

A 2007 paper by D. Cumin and C.P Unsworth noted that intrinsic frequencies of oscillators - as applied to neuronal oscillators - must be time adaptive to reflect the naturally changing threshold levels at which neurons fire. It also pointed to the need to establish the aforementioned adjacency matrix term to reflect the different types of connectivity within different clusters of neurons, which could move beyond a simple '1' or '0' value to reflect existence of links, and instead could be given a weighting to reflect both existence and strength of link/coupling. This is represented below:

$$\frac{\partial \theta_i}{\partial t} = \omega_i(t) + \sum_{j \neq i} K_{ij} \sin(\theta_j - \theta_i)$$

Bibliograph

Pérez, A., Carreiras, M. & Duñabeitia, J.A. Brain-to-brain entrainment: EEG interbrain synchronization while speaking and listening. Sci Rep **7**, 4190 (2017). https://doi.org/10.1038/s41598-017-04464-4

Pikovsky, A., Rosenblum, M., & Kurths, J. (2001). Basic notions: The self-sustained oscillator and its phase. In Synchronization: A Universal Concept in Nonlinear Sciences (Cambridge Nonlinear Science Series, pp. 27-44). Cambridge: Cambridge University Press. doi:10.1017/CB09780511755743.003

Jenkins, Alejandro (2013). 'Self-oscillation', Physics Reports, 525. pp 167.

Winfree, A. T. (1967), 'Biological rhythms and the behaviour of populations of coupled oscillators', Theor. Biol. 16(1), 15–42.

(2009) Self-sustaining Oscillation. In: Binder M.D., Hirokawa N., Windhorst U. (eds) Encyclopedia of Neuroscience. Springer, Berlin, Heidelberg.

Steven H. Strogatz (2000). From Kuramoto to Crawford: exploring the onset of synchronization in populations of coupled oscillators, Physica D: Nonlinear Phenomena (143), 1-20.

Kuramoto, Y. (1983), Chemical Oscillations, Waves and Turbulence., Spinger-Verlag, New York.

Francisco A. Rodrigues, Thomas K. DM. Peron, Peng Ji, Jürgen Kurths (2016). The Kuramoto model in complex networks, Physics Reports (610), 1-98.

Filatrella, G., Nielsen, A. & Pedersen, N. (2008), Analysis of a power grid using a Kuramoto-like model. Eur. Phys. J. B 61, 485–491.

Breakspear, M, Stewart, H & Daffertshofer, A. (2010) 'Generative Models of Cortical Oscillations: Neurobiological Implications of the Kuramoto Model', Frontiers in Human Neuroscience (4) 190.

D. Cumin, C.P. Unsworth (2007) 'Generalising the Kuramoto model for the study of neuronal synchronisation in the brain', Physica D: Nonlinear Phenomena, (226) 181-196.