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FURIOUSLY FLASHING FIREFLIES

Synchronised Signalling in the Mating Game

A Lecture by

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One of the most spectacular displays in the whole of nature occurs in South-East Asia, where huge swarms of fireflies flash in synchrony. Why do the flashes synchronise? This question is answered by introducing a mathematical model of how fireflies respond to each others' signals. The lecture will discuss this application of mathematics to biology, and related ones, in non-technical terms.

Fig.1 Synchronous flashing of fireflies in a tree.

The drama of synchronous flashing of certain species of firefly was described by the American biologist Hugh Smith in 1935:

> 'Imagine a tree thirty-five to forty feet high, apparently with a firefly on every leaf, and all the fireflies flashing in perfect unison at the rate of about three times in two seconds, the tree being in complete darkness between flashes. Imagine a tenth of a mile of river front with an unbroken line of mangrove trees with fireflies on every leaf flashing in synchronism, the insects on the trees at the ends of the line acting in perfect unison with those between. Then, if one's imagination is sufficiently vivid, he may form some conception of this amazing spectacle.'

Why do the flashes synchronise? The biological reason seems to be an evolutionary one. The flashes are created solely by male fireflies, and they attract females. Synchronised flashes attract them from further away, offering an evolutinary advantage.

What about the mathematical reason? In 1990 Renato Mirollo and Steven Strogatz showed that synchrony is the rule for mathematical models in which every firefly interacts with every other. Their idea is to model the insects, and the signals that pass between them, as a population of mathematical oscillators, coupled together by visual signals. The chemical cycle used by each firefly to create a flash of light is represented as an oscillator. The population of fireflies is represented by a network of such oscillators with fully symmetric coupling — that is, each oscillator affects all of the others in exactly the same manner. The most unusual feature of this model, which had been introduced by Charles Peskin in 1975, is that the oscillators are *pulse-coupled.* That is, an oscillator affects its neighbours only at the instant when it creates a flash of light. The mathematical difficulty is to disentangle all of these interactions. We do this by applying techniques from dynamical systems theory, in which oscillators are an especially important component. So first I shall develop some of the necessary concepts.

Oscillators

Oscillators are a source of periodic rhythms, which are common — and important — in biology. Our hearts and lungs follow rhythmic cycles whose timing is adapted to our body's needs. Many of nature's rhythms are like the heartbeat: they take care of themselves, running 'in background'. Others are like breathing: there is a simple 'default' pattern that operates as long as nothing unusual is happening, but there is also a more sophisticated control mechanism that can kick in when necessary and adapt those rhythms to immediate needs. Controllable rhythms of this kind are particularly common — and particularly interesting — in locomotion. Although the biological interactions that take place in individual animals and populations of animals are very different, there is an underlying mathematical unity, and one of the messages of this lcture is that the same general mathematical concepts can apply on many different levels and to many different things. Nature respects this unity, and makes good use of it.

The organising principle behind these biological cycles, and many like them, is the mathematical concept of an *oscillator* — a unit whose natural dynamic causes it to repeat the same cycle of behaviour over and over again. Biology hooks together huge 'circuits' of oscillators, which interact with each other to create complex patterns of behaviour. Such 'coupled oscillator networks' are a central research topic in today's mathematics.

Why do systems oscillate? Oscillation is the simplest thing you can do if you don't want, or are not allowed, to remain still. Why does a caged tiger pace up and down? Its motion results from a combination of two constraints. First, it feels restless and does not wish to sit still. Second, it is confined within the cage and cannot simply disappear over the nearest hill. The simplest thing you can do when you have to move but can't escape altogether is to oscillate. Of course there is nothing that forces the oscillation to repeat a regular rhythm; the tiger is free to follow an irregular path round the cage. But the simplest option — and therefore the one that is most likely to arise both in mathematics and in nature — is to find some series of motions that works, and repeat it over and over again. And that is what we mean by a periodic oscillation. A more physical example is the vibration of a violin string. That, too, moves in a periodic oscillation; and it does so for the same reasons as the tiger. It can't remain still because it has been plucked away from its natural resting point; and it can't get away altogether because its ends are pinned down and its total energy cannot increase.

There are at least two distinct ways in which oscillations can arise. Many oscillations grow from steady states. As conditions change, a system that has a steady state may lose it and begin to wobble periodically. In 1942 the German mathematician Eberhard Hopf found a general mathematical condition that guarantees such behaviour: in his honour this scenario is known as *Hopf bifurcation*.

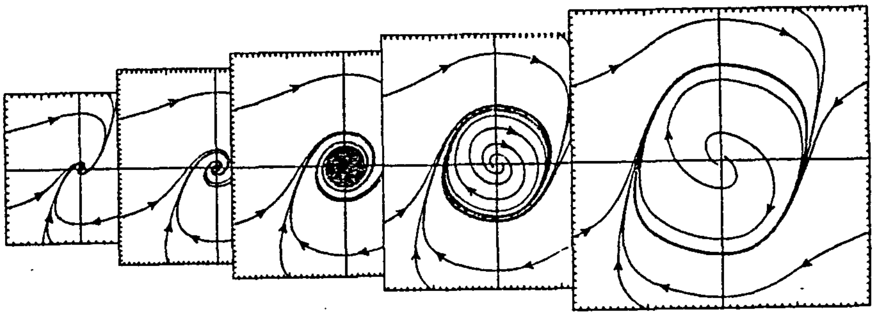

Fig.2 Creation of an oscillation by Hopf bifurcation.

The workings of a clarinet, for example, depend upon Hopf bifurcation: as the clarinettist blows air across the instrument's reed, the reed ceases to remain steady and begin to vibrate. This vibration is transmitted to the air, and the vibrating air is what we hear as music. Hopf bifurcation can be seen as a special type of *symmetry-breaking*. This is a general mechanism for pattern formation, in which a symmetric system adopts states that are not fully symmetric because the symmetric state is unstable. In Hopf bifurcation, the symmetries that break relate not to space, but to time. Time is a single variable, so mathematically it corresponds to a line, the time axis. There are only two types of symmetry of a line: translations and reflections. What does it mean for a system to be symmetric under time translation? It means that if you observe the motion of the system, or wait for some fixed interval of time and *then* observe the motion of the system, you see exactly the same behaviour. But that is a description of periodic oscillations: if you wait for an interval of time that is equal to the period, you see exactly the same thing. So periodic oscillations have time-translation symmetry.

The oscillations of fireflies are not created by Hopf bifurcation, but by a second mechanism known as 'integrate-and-fire'. In such oscillators some quantity builds up until it reaches some *threshold.* This triggers a sudden change in which the quantity is reset to a much lower value, after which the build-up occurs again. In the firefly, this quantity is the amount of chemical needed to produce a flash. Once the fly has stockpiled enough chemical, it uses it up in a flash and the whole process starts again.

Another physical example of such an oscillator is the build-up of electric charge in a capacitor, which discharges when the total charge reaches some specific threshold.

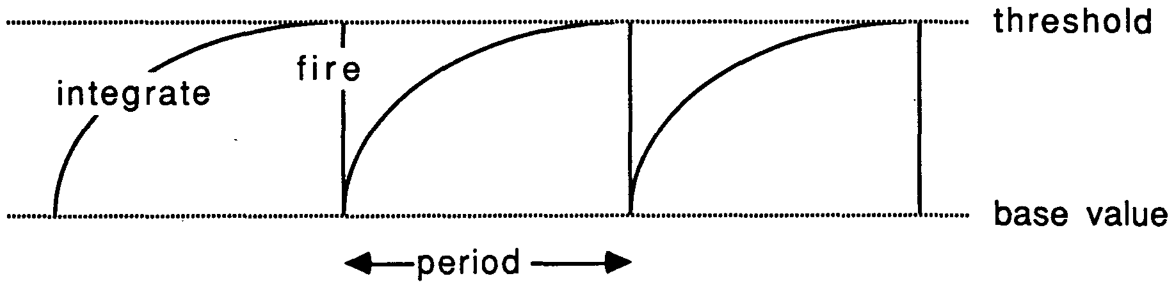

Fig.3 Integrate-and-fire oscillator.

In 1975 Charlie Peskin, a physiologist, introduced a specific model of an integrate-and-fire oscillator in a study of the synchronisation of the muscle fibres of the heart. His model is a differential equation, *Peskin's equation*:

$$\frac{dx}{dt} = S - \gamma x$$

where S and γ are constants > 0, together with a 'firing rule':

if $x(t) = 1$ at some time t then it is reset to $x(t) = 0$.

This same model applies to fireflies, and is justified by physiological studies.

Coupling

Oscillators are said to be *coupled* if each affects the state of the other. The classic example is the observation, made by Christiaan Huygens, that pendulum clocks on the same shelf of a clockmaker's shop affect each other (through vibrations of the shelf). Often the result is that they synchronise. However, coupled oscillators do not always synchronise, an example being an animal's legs when it walks. Each leg is an oscillator, and the animal's body couples them, but they do not normally all move at once.

Peskin introduced the idea of *pulse coupling* for integrate-and-fire oscillators. Here the oscillators affect each other only when one fires. Then it sends some signal to the others, which adjusts their states. Suppose oscillator i is coupled to oscillator j, their states at time t being represented by the quantitites $x_i(t)$ and $x_j(t)$. Assume that oscillator i reaches threshold and fires. Then

$x_i(t)$ is reset to 0

and Peskin required that

$x_j(t)$ is 'pulled up' by an amount ε, becoming $x_j(t)+\varepsilon$.
If this exceeds threshold, then it too is reset to 0.

It turns out that the chemicals in fireflies are affected in just this manner by signals from other fireflies. When a firefly sees another one flash then it gets excited and produces more of its luminescent chemical!

Peskin proved that if two identical integrate-and-fire oscillators are pulse-coupled, then for almost all initial conditions they will eventually synchronise. I will prove this below. He also conjectured that the same would be true of any network of coupled integrate-and-fire oscillators.

Two Oscillators

We can solve Peskin's equation explicitly, getting

$$x=\frac{S}{\gamma}(1-e^{-\gamma t}).$$

This formula can be used to calculate how the coupled oscillator system behaves. For example the period T satisfies

$$1=\frac{S}{\gamma}(1-e^{-\gamma T}),$$

since the threshold value is (by convention) x = 1. So we get

$$T=\frac{1}{\gamma}\log\frac{S}{S-\gamma}.$$

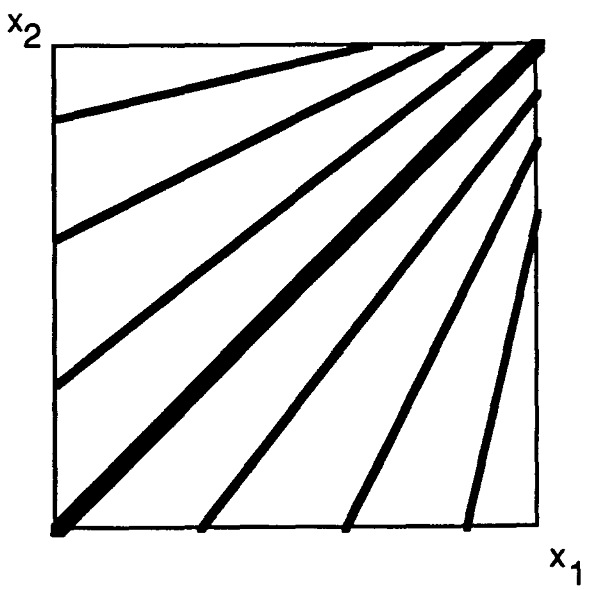

Fig.4 Phase portrait of a two-oscillator system, no coupling.

First suppose that we have two oscillators x_1 and x_2, both satisfying Peskin's equation. To begin with, ignore the coupling. Then we can apply the formula and plot how the combined values $(x_1(t), x_2(t))$ vary with t. The result, called a *phase portrait*, is shown in Fig.4. The synchronised state, $x_1 = x_2$, is represented by the diagonal line.

We can represent the firing rule graphically by adding a 'margin' of width ε to the picture, in which one oscillator fires and the other is pulled up by ε, as in Fig.5. Traversing the margin takes zero time.

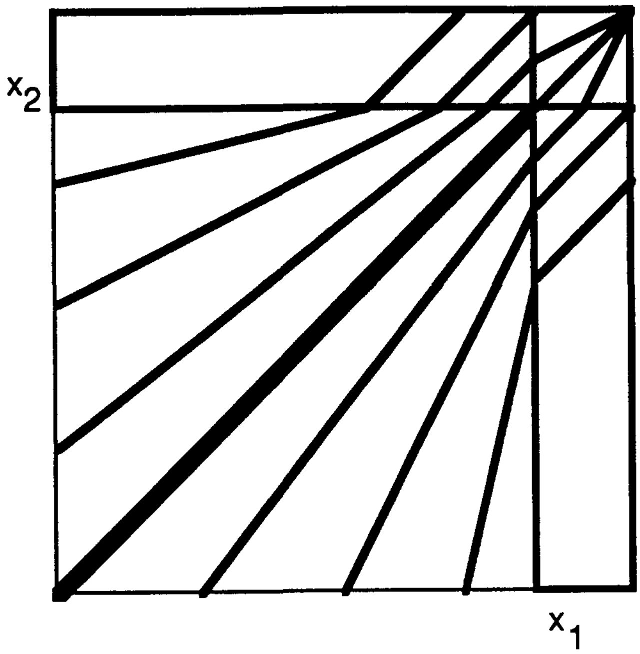

Fig.5 Phase portrait of a two-oscillator system, coupling added.

Finally, we 'wrap round' to show the periodicity, as in Fig.6.

Now we can read off the behaviour. Initial states in the region labelled '1' synchronise after one firing. Those in region 2 synchronise after two firings, and so on. It looks as if the entire region labelled '...' fills up with states that syncrhonise. Using Peskin's formula this can be checked — note, however, that there is a line of states running through the middle of that region that represents a periodic *unsynchronised* state. However, it is unstable.

Mirollo and Strogatz proved that with a more general law than Peskin's, and with a system of *n* identical integrate-and-fire pulse-coupled oscillators with 'all to all' coupling, then no matter what the initial conditions are, eventually all of the oscillators become synchronised. The proof is based on the idea of *absorption*, which happens when two oscillators with different phases 'lock together' and thereafter stay in phase with each other. Because the coupling is fully symmetric, once a group of oscillators has locked together, it cannot unlock. A geometric and analytic proof shows that a sequence of these absorptions must eventually lock *all* of the oscillators together.

In other networks, more complicated patterns are possible — including chaos.

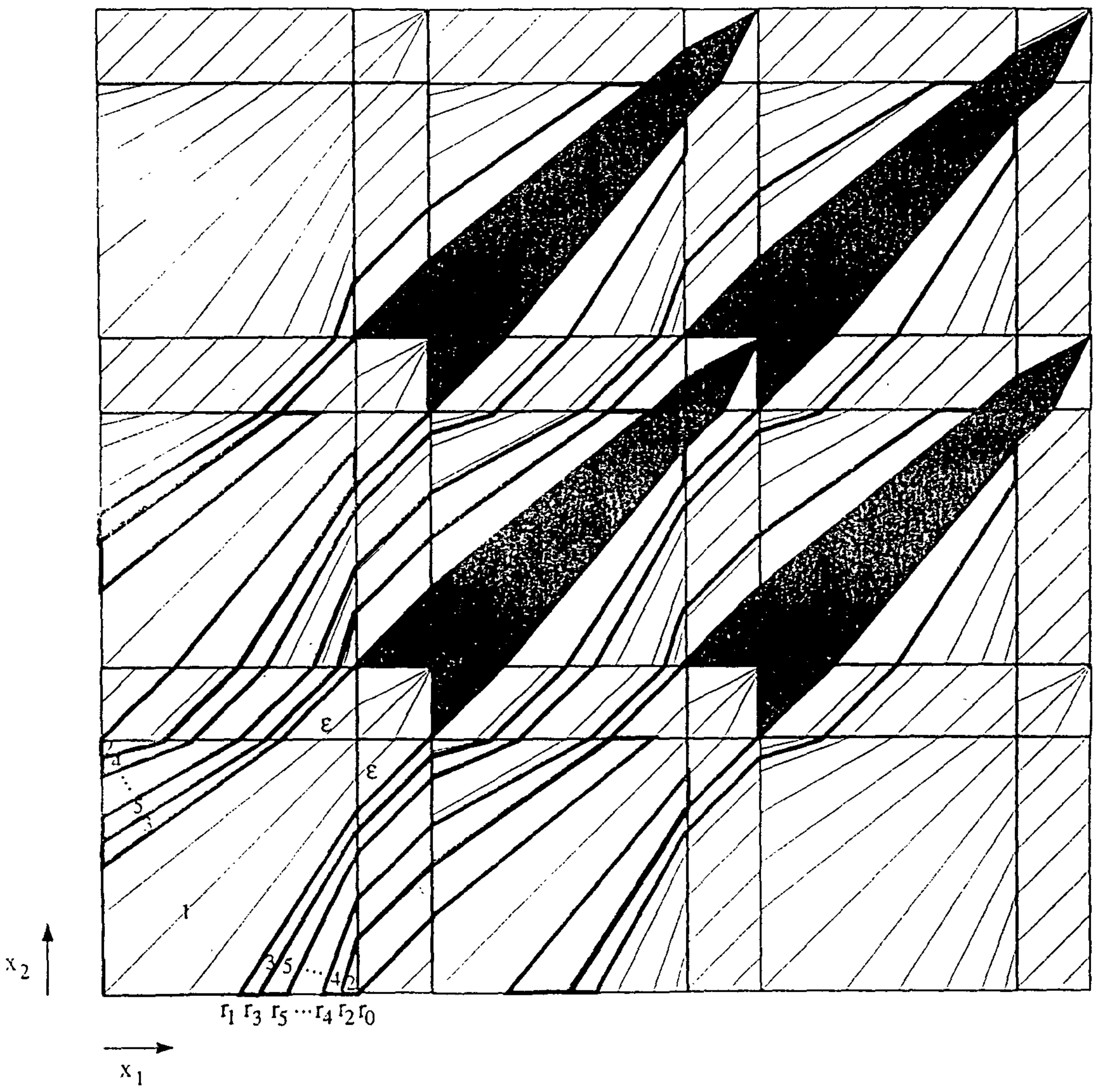

Fig.6 Phase portrait of a coupled two-oscillator system wrapped round to show periodicity. Numbering shows how various initial states synchronise.

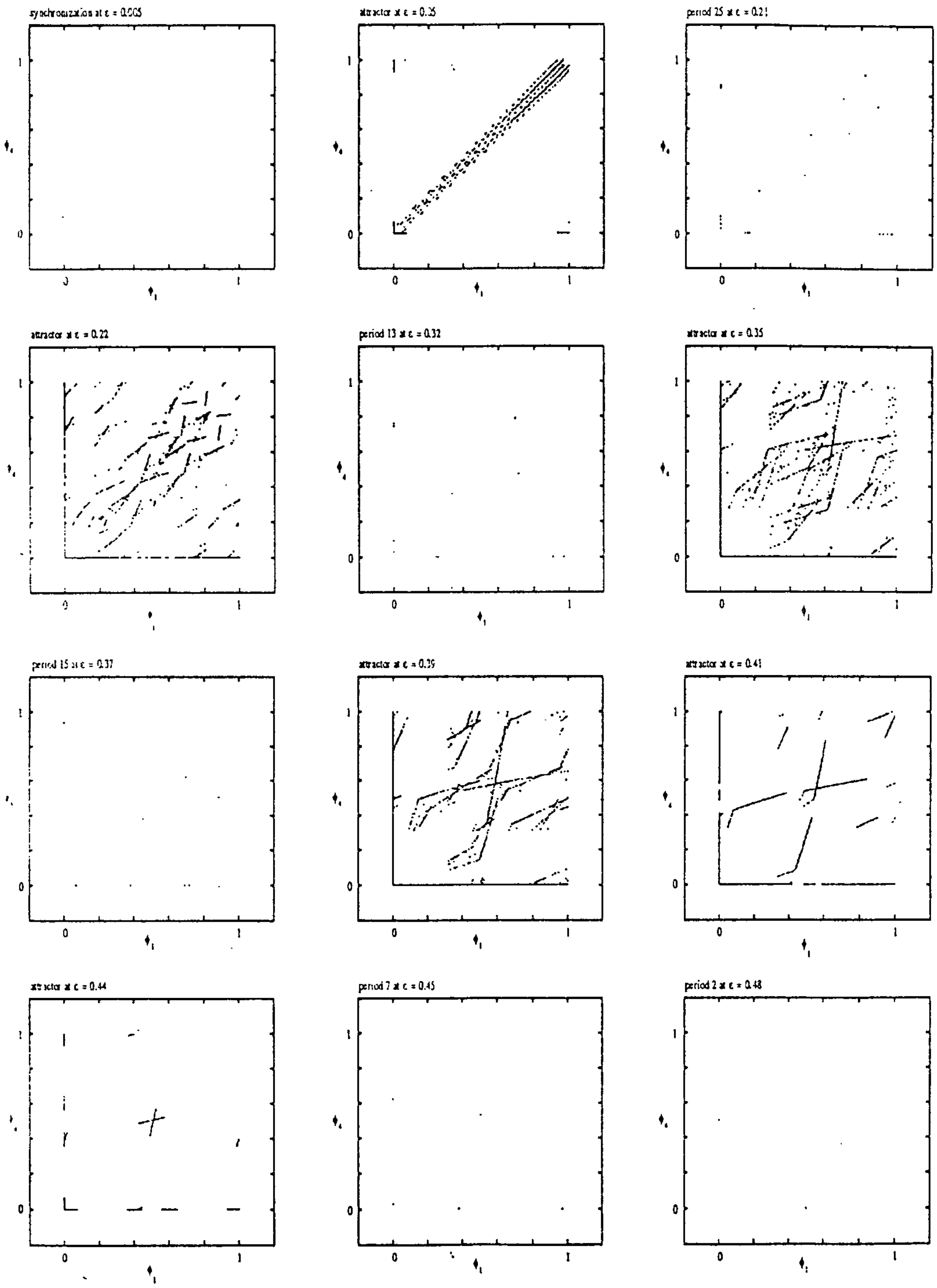

Fig.7 Phase portraits of a 4-oscillator system coupled in a ring show perodicity and chaos.

These ideas apply to many systems other than fireflies. Applications include the pacemaker cells of the heart; networks of neurons in the brain, including those controlling circadian rhythms; the insulin-secreting cells in the pancreas; crickets and katydids that chirp in unison; and groups of women whose menstrual periods become synchronised.

And, as a Rugby bus driver pointed out to me, it is also closely related to the phenomenon whereby you wait for a bus and none come, until suddenly three come along at once.

Synchronised buses!

FURTHER READING

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Gresham College was established in 1597 under the Will of the Elizabethan financier Sir Thomas Gresham, who nominated the Corporation of the City of London and the Worshipful Company of Mercers to be his Trustees. They manage the Estate through the joint Grand Gresham Committee. The College has been maintained in various forms since the foundation. The one continuing activity (excepting the period 1939-45) has been the annual appointment of seven distinguished academics "sufficiently learned to reade the lectures of divyntye, astronomy, musicke, and geometry" (appointed by the Corporation), "meete to reade the lectures of lawe, phissicke, and rethoricke", (appointed by the Mercers' Company). From the 16th century the Gresham Professors have given free public lectures in the City. A Mercers' School Memorial Chair of Commerce has been added to the seven 'ancient' Chairs.

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