NORBERT WIENER'S BRAIN WAVES

STEVEN H. STROGATZ

Department of Mathematics
Massachusetts Institute of Technology
Cambridge, MA 02139, USA

INTRODUCTION

In the late 1950's Norbert Wiener became interested in the spectrum of human brain waves (Wiener 1958, 1961). Along with his medical collaborators, he made high-resolution electroencephalographic recordings from subjects who were awake but resting with their eyes closed. Under these conditions, the electroencephalogram shows conspicuous activity at frequencies around 10 Hz – the so-called alpha rhythm.

Figure 1 shows Wiener's sketch of the magnified spectrum around 10 Hz. He writes:

> It would have been quite conceivable that there would not be a phenomenon of that sort; i.e., it might have been that all our work on the fine structure of the brain waves was wasted. However, once we find this effect, we are under an obligation to try to give an explanation of it. There are two things that are striking here: One is the very narrow line at the center of the spectrum, and the other is that this line arises from a dip.

To explain this spectrum, Wiener hypothesized that there is a population of oscillators in the brain whose intrinsic frequencies are close to 10 Hz and that these oscillators "constitute a more accurate oscillator *en masse* than they do singly." The idea is that the oscillators interact by pulling on each other's frequencies – if an oscillator is ahead of the group, the group tends to slow it down. If it is going too slowly, the group tends to speed it up. In this way the population of oscillators can achieve a collective enhancement of precision.

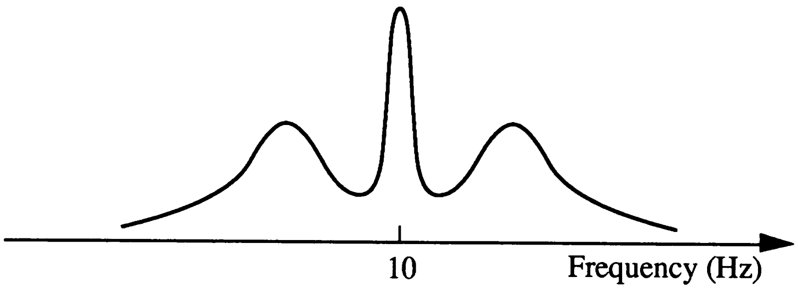


Fig.1. Wiener's schematic sketch of the spectrum of human alpha waves, redrawn from Wiener (1958, p.69).

Wiener (1958) tried to support his notion of frequency-pulling with the experimental evidence available in those days. For instance, he mentions an amazing experiment involving direct electrical driving of the brain. A sheet of tin was suspended from the ceiling and connected to one terminal of a 400-volt, 10 Hz generator. He writes that this apparatus "can produce electrostatic induction in anything in the room" and that "it can actually drive the brain, causing a decidedly unpleasant sensation."(!)

It is probably wise to take Wiener's experimental claims with a grain of salt. He rarely shows or cites actual data – Fig. 11 in Wiener (1961) is the lone exception – and as far as I know, no one has ever replicated his results. Wiener (1958) also attempted to account for his observations mathematically, but his approach was awkward and led nowhere. However, he did leave an important legacy: he was the first to propose studying the collective behavior of biological oscillators.

In the years since Wiener's work, it has become clear that mutual synchronization is ubiquitous in biology (Winfree 1967, 1980, 1987). Examples include pacemaker cells in the heart (Peskin 1975; Michaels et. al 1987), glycolytic synchrony in yeast cell suspensions (Ghosh et. al 1971; Aldridge and Pye 1976), collective oscillations of pancreatic beta cells (Sherman and Rinzel 1991), synchronously flashing fireflies (Buck 1988), crickets that chirp in unison (Walker 1969) and women whose menstrual cycles become mutually synchronized (McClintock 1971). We review some of these examples in Sect. 2, and then in Sect. 3 we consider the classic model of mutual synchronization. The analysis of this model over the past twenty-five years has drawn on a wonderful range of subjects: nonlinear dynamics of course, but also statistical mechanics and even plasma physics! As we'll see, Norbert Wiener's spectrum has *almost* been explained in a mathematical sense – but not quite. Many other tantalizing problems remain for both theory and experiment, as discussed in Sect. 4.

2. BIOLOGICAL EXAMPLES

2.1 Menstrual Synchrony

Everyone has heard of the phenomenon of synchronized menstrual cycles among women friends or roommates (Anonymous 1977). The first scientific study of menstrual synchrony was carried out by Martha McClintock (1971) while she was an undergraduate psychology major at Radcliffe in the late 60's. She studied 135 women undergraduates and had them keep records of their periods throughout the school year. In October, the cycles of close friends and roommates started an average of 8.5 days apart, but by March, the average spacing was down to five days, a statistically significant change. Randomly matched pairs of women showed no such change.

There are various ideas about the mechanism of synchronization, but the best guess is that it has something to do with sweat! Apparently there's some (unknown) substance in sweat that conveys a synchronizing signal. The evidence for this comes from an experiment by Michael Russell (1980). A colleague of his, Genevieve Switz, had noticed the synchrony effect in her own life – when rooming with a female friend of hers during the summer, the friend's period would lock on to hers, then drift apart after they separated in the fall. This suggested that Genevieve was a powerful entrainer.

Russell tried to determine what it was about Genevieve that was so compelling. For the experiment, Genevieve wore small cotton pads under her arms and then donated the accumulated sweat to Russell each day. He then mixed it with a little alcohol and dabbed this "essence of Genevieve" on the upper lip of female subjects, three times a week for four months.

The results were startling: after four months, the subjects' periods began an average of 3.4 days apart from Genevieve's, down from 9.3 days at the beginning of the experiment. In contrast, the cycles of a control group (whose upper lips were dabbed with alcohol only) showed no significant change. Evidently something in Genevieve's sweat conveyed information about the phase of her menstrual cycle, in such a way that it tended to entrain the cycles of the other women who got wind of it.

Now I know that this all sounds unbelievable, even more so because Genevieve's last name seems phony – doesn't Switz remind you of the German word for "sweat"? Anyway, this is what has been reported.

2.2 Fireflies

In the animal world, groups of Southeast Asian fireflies provide a spectacular example of synchronization. Along the tidal rivers of Malaysia, Thailand and New Guinea, thousands of fireflies congregate in trees at night and flash on and off in unison. When they first arrive, their flickerings are uncoordinated. But as the night goes on, they build up the rhythm until eventually whole treefuls pulsate in silent concert. You can see this display on David Attenborough's (1992) television show *The Trials of Life* in the episode called "Talking to Strangers." As he explains, "All those that are flashing are males, and their message, of course, is directed to the females, and it's a very simple one: 'Come hither – mate with me'." The evolutionary significance of this group synchrony is controversial; see Buck (1988) for a review of the various theories, and for more information about synchronous fireflies.

The fireflies use visual information to achieve entrainment – they see each others' flashes and adjust their rhythm accordingly – but the details differ across species. These differences can be probed by flashing a light periodically at an individual firefly, and measuring the timing of its flashes as it tries to get in step. For driving frequencies close to its natural frequency, the species *Pteroptyx cribellata* can phase-lock but with a non-zero phase difference; it lags a faster stimulus and leads a slower one (Hanson 1978). In contrast, the grandmaster of synchronization, *Pteroptyx malaccae*, can match both frequency *and* phase. It manages to flash almost simultaneously with the stimulus, even if the driving frequency differs by up to 15% from its natural frequency (Hanson 1978; Buck 1988). This suggests that the firefly can "learn" the frequency of the driver. This idea is further supported by the observation that when the drive is turned off, the firefly continues to flash at that frequency for several cycles before relaxing back to its native frequency (Ermentrout 1992).

2.3 Yeast and Gonyaulax

Much simpler creatures, all the way down to unicellular organisms, are also capable of mutual synchronization. For example, suspensions of yeast cells can exhibit synchronous sugar metabolism. Normally yeast cells convert sugar to alcohol in a steady trickle, but under contrived laboratory conditions, they can be made to exhibit glycolytic oscillations with a period around 30 seconds (Ghosh et. al 1971; Winfree 1980, 1987). The oscillations can be monitored optically, because one of the metabolic intermediates conveniently fluoresces under ultraviolet light. In a beaker full of thousands of such cells, the oscillations occur in rigid lockstep. It is thought that the cells communicate chemically through diffusion of acetaldehyde, pyruvate, or some other substance. To gain further information about the coupling, Ghosh et. al (1971) mixed two different beakers of cells, synchronous within themselves but differently phased from each other. They found that the mixture rapidly re-established synchrony, but at a compromise phase that depended in a subtle way on the parent phases. See (Winfree 1980, 1987) for a topological discussion of the resetting map.

To be honest, we should mention that in many populations of biological oscillators, the coupling is insufficient to enforce synchrony, or it may actively *oppose* synchrony (Winfree 1967). The cells in our bodies are undergoing asynchronous cell division all the time, and in spite of what the song says about "two hearts that beat as one," there are no documented cases of mutual cardiac entrainment.

But these failures may be too extreme – it is more interesting to consider populations that barely miss achieving synchrony. One such example is the bioluminescent alga *Gonyaulax*, which lights up as you swim through it at night in southern California and elsewhere. If a tank full of *Gonyaulax* is brought from the ocean and then kept in constant darkness in a laboratory, it exhibits a circadian glow rhythm with a period close to 23 hours. However, this rhythm gradually damps out and the waveform broadens as the days go by. Njus et. al (1984) argued that this broadening is due to desynchronization – the individual cells continue to oscillate but they drift out of phase, either because of differences in their natural frequencies or because of cycle-to-cycle variability within each individual. Furthermore, when one tries the analog of the yeast mixing experiment on this organism, the ingredient populations maintain their identities for over a week, though there's some indication of mutual influence in the second week (Hastings et. al 1985).

3. THE CLASSIC MODEL

3.1 Winfree's Work

In his first publication (1967), Art Winfree proposed the theoretical approach that still guides us today. Like Wiener, he explored large systems of coupled oscillators. Of course, such systems had been studied for decades in physics, but Winfree recognized that the biological problem required a new set of assumptions. In many-body physics, the oscillators are usually conservative and identical; in biology, the oscillators are self-sustained and non-identical. By "self-sustained" we mean that each oscillator has a stable limit cycle, corresponding to the individual's free-running oscillation. This assumption is appropriate because biological oscillators generally regulate their amplitude – if perturbed, they return to a standard cycle, whereas conservative oscillators would remember such perturbations forever. Moreover, biological oscillators are never identical, thanks to genetic variability, etc.

So to achieve even minimal biological realism, one needs to study a population of coupled limit-cycle oscillators with randomly distributed properties. As stated, this problem is too hard. Winfree (1967) pointed out that the problem would simplify if the oscillators were *weakly* coupled (compared to the attractiveness of their limit cycles). Then the oscillators would never move far from their limit cycles, so each could be described solely in terms of its phase along the cycle. Thus, Winfree invented what is known today as the "phase model" approximation. Two other important simplifications: (i) He assumed that the intrinsic frequencies were distributed at random across the population, but that the oscillators were identical in all other respects. (ii) Each oscillator was assumed to be influenced by the collective rhythm produced by *all* the others. For example, in the case of fireflies this means that each firefly responds to the collective flash of the whole population, rather than to any individual firefly. Mathematically, this amounts to a mean-field approximation, which is always the simplest place to start when analyzing a new many-body system (Ma 1985).

Through numerical and analytical studies, Winfree discovered that synchronization occurs *cooperatively*, in a manner strikingly reminiscent of a thermodynamic phase transition. When the spread of natural frequencies is large compared to the coupling, the oscillators behave incoherently, with each running at its natural frequency. As the spread is decreased, the population remains incoherent until, below a critical spread, the system spontaneously "freezes" into synchrony.

3.2 Kuramoto's Model and Analysis

The analogy between synchronization and phase transitions stimulated a great deal of interest among statistical physicists. In particular, Yoshiki Kuramoto (1975, 1984) proposed a beautiful and analytically tractable model based on Winfree's ideas. The peculiar spectrum (Fig. 1) found by Wiener (1958) pops out of the analysis, as does a formula for the synchronization threshold discussed by Winfree (1967). But beware – Kuramoto's analysis is like many of the best arguments of physics: bold, ingenious, but far from rigorous. Indeed, it raises conceptual subtleties that are still not understood, as we'll discuss later.

Kuramoto considered the following system:

$$\dot{\theta}_i = \omega_i + \frac{K}{N}\sum_{j=1}^{N}\sin(\theta_j - \theta_i) \tag{1}$$

where $i = 1, \cdots, N$. Here $\theta_i(t)$ is the phase of the oscillator i, $K \geq 0$ is the coupling strength, and the natural frequencies ω_i are distributed according to a probability density $g(\omega)$. The sinusoidal coupling tends to synchronize the oscillators; if θ_j is slightly ahead of θ_i, the sine term tends to speed θ_i up and slow θ_j down. Thus the oscillators pull on each other's frequencies in the way envisaged by Wiener (1958). Each oscillator is coupled to all the others with a strength of K/N, where the factor $1/N$ ensures that the system has a non-trivial limiting behavior as $N \to \infty$.

The probability density $g(\omega)$ is assumed to be unimodal and symmetric about a mean frequency Ω, i.e., $g(\Omega + \omega) = g(\Omega - \omega)$. From now on we assume that $\Omega = 0$; otherwise we may redefine all phases by $\theta_i \to \theta_i + \Omega t$. This leaves (1) invariant, but effectively subtracts Ω from all the ω_i, and therefore shifts the mean of $g(\omega)$ to zero. Physically this corresponds to going into a rotating frame at the mean frequency. The advantage is that phase-locked solutions with frequency Ω in the original frame now appear as fixed points in the rotating frame.

To visualize the dynamics of (1), imagine a swarm of points moving around the unit circle in the complex plane. It's convenient to introduce the centroid of the swarm, given by

$$re^{i\Psi} = \frac{1}{N}\sum_{j=1}^{N} e^{i\theta_j}, \tag{2}$$

as shown in Fig. 2. Here $r \geq 0$ measures the phase coherence of the oscillators, and Ψ is the average phase. Notice that $r \approx 0$ if the oscillators are randomly spread around the circle and $r \approx 1$ if they're nearly in phase. Therefore r is called the "order parameter" for the system.

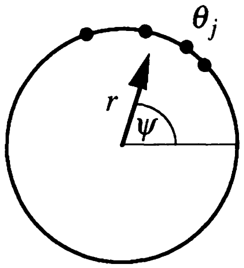


Fig. 2. Geometric interpretation of the order parameter. The phases θ_j are plotted as points on the unit circle. Their centroid is given by the complex number $re^{i\Psi}$, shown as an arrow.

If we integrate (1) numerically, how does $r(t)$ evolve? For concreteness, suppose that $g(\omega)$ is a Gaussian or some other density with infinite tails. Then for all K less than a certain threshold K_c, the oscillators act almost as if they were uncoupled: for any initial condition, $r(t)$ decays to a jitter of size $O(N^{-1/2})$, reflecting incoherent motion of the θ_i (Fig. 3).

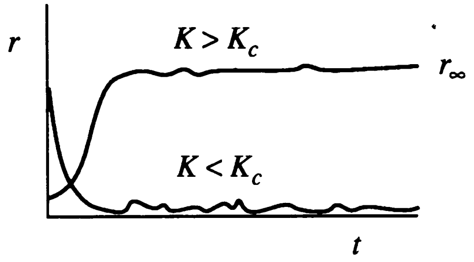


Fig. 3. Typical evolution of $r(t)$ seen in numerical integrations of (1).

But when K exceeds K_c, incoherence becomes unstable and $r(t)$ grows exponentially, indicating the onset of spontaneous synchronization (Fig. 3). Ultimately $r(t)$ saturates to some final value r_∞, though again with fluctuations of size $O(N^{-1/2})$. At the level of the individual oscillators, one finds that those near the the center of the distribution have mutually synchronized, whereas those in the tails remain wild and run near their natural frequencies. With further increases in K, more and more oscillators are recruited into the synchronous pack, and r_∞ grows as shown in Fig. 4.

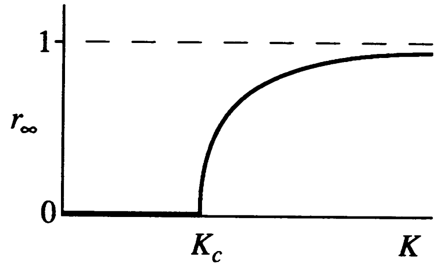


Fig. 4. Dependence of steady-state coherence r_∞ on coupling strength K. A continuous phase transition occurs at $K = K_c$.

Kuramoto's analysis begins with the observation that, thanks to a trigonometric identity, (1) can be rewritten in terms of the centroid as

$$\dot{\theta}_i = \omega_i + Kr\sin(\Psi - \theta_i), \tag{3}$$

for $i = 1, \cdots, N$. In the limit $N \to \infty$, numerical simulations suggest that $r(t)$ always approaches a constant as $t \to \infty$. Moreover, in our rotating frame, $\Psi(t)$ also seems to approach a constant. Here comes the *first bold move:* seeks solutions of (3) for which both r and Ψ are constant. Without loss of generality, we may choose coordinates such that $\Psi = 0$.

Then (3) has two types of solution, depending on the relative size of ω_i and Kr. If $|\omega_i| \leq Kr$, then (3) has a stable fixed point at θ defined by

$$\omega_i = Kr\sin\theta_i, \tag{4}$$

for $|\theta_i| \leq \pi/2$. These oscillators will be called "locked" because in the original frame they are phase-locked at frequency Ω. On the other hand, the oscillators with $|\omega_i| > Kr$ run around the circle periodically, hesitating at some phases and accelerating at others; they are called the "drifting" oscillators. As expected, the locked oscillators correspond to the center of the frequency distribution, while the drifting oscillators correspond to the tails.

Now comes the crux of the matter: the existence of drifting oscillators seems to be inconsistent with the assumption that the order parameter (2) is time-independent. How can r be constant with all those oscillators buzzing around the circle? Kuramoto sidestepped this problem with a *second bold move:* he demanded that for each ω, the oscillators of that frequency form a *stationary distribution* $\rho(\theta, \omega)$ on the circle. Then even though individual oscillators continue to move, the centroid of the system stays constant. For stationarity, $\rho(\theta, \omega)$ must be inversely proportional to the velocity; oscillators bunch up at slow places on the circle and spread out at fast places. Hence

$$\rho(\theta, \omega) = \frac{C}{|\omega - Kr \sin\theta|}. \tag{5}$$

The normalization constant C is determined by $\int_{-\pi}^{\pi} \rho(\theta, \omega) d\theta = 1$ for each ω, which yields $C = (2\pi)^{-1}(\omega^2 - K^2 r^2)^{1/2}$.

Next we invoke a *self-consistency* condition: the constant r assumed throughout must be consistent with that implied by (4, 5). Since $\Psi = 0$, the consistency condition is $r = \langle e^{i\theta} \rangle$, where the brackets denote an average over the population. This average contains two separate contributions r_{lock} and r_{drift}, which we calculate in turn. As $N \to \infty$, the law of large numbers implies

$$r_{lock} \to \int_{-Kr}^{Kr} \exp[i\theta(\omega)] g(\omega) d\omega,$$

where $\theta(\omega)$ is defined implicitly by (4). The imaginary part of this integral vanishes because $\sin\theta(\omega)$ is odd in ω, whereas $g(\omega)$ is even by assumption. Hence

$$r_{lock} = \int_{-Kr}^{Kr} \cos\theta(\omega) g(\omega) d\omega.$$

Changing variables from ω to θ yields

$$\begin{aligned} r_{lock} &= \int_{-\pi/2}^{\pi/2} \cos\theta g(Kr\sin\theta) Kr \cos\theta d\theta \\ &= Kr \int_{-\pi/2}^{\pi/2} \cos^2\theta g(Kr \sin\theta) d\theta. \end{aligned}$$

Now consider the drifting oscillators. They contribute

$$r_{drift} = \int_{-\pi}^{\pi} \int_{|\omega|>Kr} \cos\theta \rho(\theta,\omega) g(\omega) d\omega d\theta.$$

Miraculously this integral vanishes! This follows from $g(\omega) = g(-\omega)$ and the symmetry $\rho(\theta + \pi, -\omega) = \rho(\theta, \omega)$ impled by (5).

Hence $r = r_{lock}$ and so the self-consistency condition reduces to

$$r = Kr \int_{-\pi/2}^{\pi} \cos^2\theta g(Kr\sin\theta) d\theta. \tag{6}$$

Equation (6) has a trivial solution $r = 0$ for all values of K. This corresponds to a completely incoherent state, with the oscillators of each frequency uniformly distributed around the circle and rotating at their natural frequencies. A second branch of solutions is defined implicitly by

$$1 = K \int_{-\pi/2}^{\pi/2} \cos^2\theta g(Kr\sin\theta) d\theta \tag{7}$$

where $r \geq 0$. This branch corresponds to partially synchronized solutions. It bifurcates continuously from $r = 0$ at a value $K = K_c$ obtained by letting $r \longrightarrow 0$ in (7). Thus

$$K_c = 2/\pi g(0),$$

which is Kuramoto's exact formula for the synchronization threshold. Moreover, by expanding the integrand in (7) in powers of r, we find $r \propto (K - K_c)^{1/2}$ close to K_c. (Here we're assuming $g''(0) < 0$, which is generic for unimodal, even densities $g(\omega)$.) For the special case $g(\omega) = (\gamma/\pi)(\gamma^2 + \omega^2)^{-1}$, Kuramoto finds that $r = \sqrt{1 - (K_c/K)}$ for all $K \geq K_c$. These formulas are in excellent agreement with numerical results (Sakaguchi and Kuramoto 1986).

An idealized version of Wiener's spectrum (Fig. 1) also emerges from this analysis. The corresponding quantity in the model is the density of modified frequencies $G(\tilde{\omega})$, where $\tilde{\omega}$ differs from ω because of frequency pulling. The locked oscillators all have $\tilde{\omega} = 0$ (or $\tilde{\omega} = \Omega$ in the original frame). They produce a delta function in $G(\tilde{\omega})$, analogous to the sharp central peak in Wiener's spectrum. The drifting oscillators have $\tilde{\omega} = \pm(\omega^2 - K^2r^2)^{1/2}$. They satisfy $|G(\tilde{\omega})d\tilde{\omega}| = |g(\omega)d\omega|$, and therefore

$$G(\tilde{\omega}) = g\left(\sqrt{\tilde{\omega}^2 + K^2r^2}\right) \left| \frac{\tilde{\omega}}{\sqrt{\tilde{\omega}^2 + K^2r^2}} \right|$$

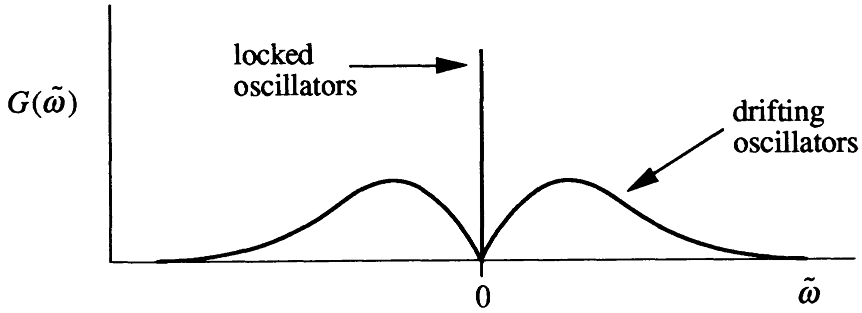


Fig. 5. The density $G(\tilde{\omega})$ of coupling-modified frequencies, as predicted by Kuramoto's model. Compare Wiener's sketch in Fig. 1.

for $|\omega| > Kr$. Thus $G(\tilde{\omega})$ is proportional to $|\tilde{\omega}|$ as $\tilde{\omega} \to 0$, and $G(\tilde{\omega}) \approx g(\omega)$ as $|\tilde{\omega}| \to \infty$. Hence $G(\tilde{\omega})$ has the shape shown in Fig. 5.

3.3 Afterthoughts

The intuitive leaps in Kuramoto's analysis deserve our admiration, but they have also provoked some vigorous head-scratching. For example, what is one to make of Kuramoto's assumption that r is constant? Surely this can never be strictly true if N is finite, but in some sense it must be *approximately* true for large N – yet in what sense? The theorem must be something like this: For most initial conditions, for most realizations of the ω's, and for a large fraction of the time, $r(t)$ stays within $O(N^{-1/2})$ of the constant $r_\infty(K)$ given by Kuramoto's analysis. It's an open problem to make this precise.

The issue could be difficult – as Nancy Kopell has pointed out, it may be connected to questions about the foundations of statistical mechanics, irreversibility, Poincaré recurrence, etc. (Keller and Bonilla 1986). To see why, consider the simple case of uncoupled oscillators ($K = 0$). Then for almost all realizations of the ω's, the phases evolve under irrational flow on an N-torus. Hence $r(t)$ should be $O(N^{-1/2})$ *most* of the time, but a few times during the life of the universe, $r(t)$ will blip up to $r \approx 1$, because the orbit is dense on the torus and therefore eventually comes close to the in-phase state. Would an analogous form of Poincaré recurrence occur if $K \neq 0$? Or is the recurrence peculiar to the special value $K = 0$, at which the system suddenly acquires a Hamiltonian structure?

Another subtle issue about finite N concerns the amplification of fluctuations for $K \approx K_c$. Such fluctuations have been addressed by Kuramoto and Nishikawa (1987) and Daido (1990), but the matter is far from resolved.

Even at the formal level of infinite-N, there are mysterious aspects to Kuramoto's analysis. What exactly is the dynamical system being studied – where did the density $\rho(\theta, \omega)$ come from? And what about the *stability* of the incoherent ($r = 0$) and partially synchronized ($r > 0$) states? Numerics indicate that $r = 0$ is globally stable for $K < K_c$, and unstable for $K > K_c$, while the partially synchronized state appears to be globally stable for $K > K_c$. How can one approach these stability questions analytically?

Recently there's been some encouraging progress. Rennie Mirollo and I have found a natural infinite-dimensional analog of Kuramoto's model (Mirollo and Strogatz 1991).

It's an evolution equation for the density $\rho(\theta, t, \omega)$ of oscillators at phase θ at time t, for each natural frequency ω. The equation is

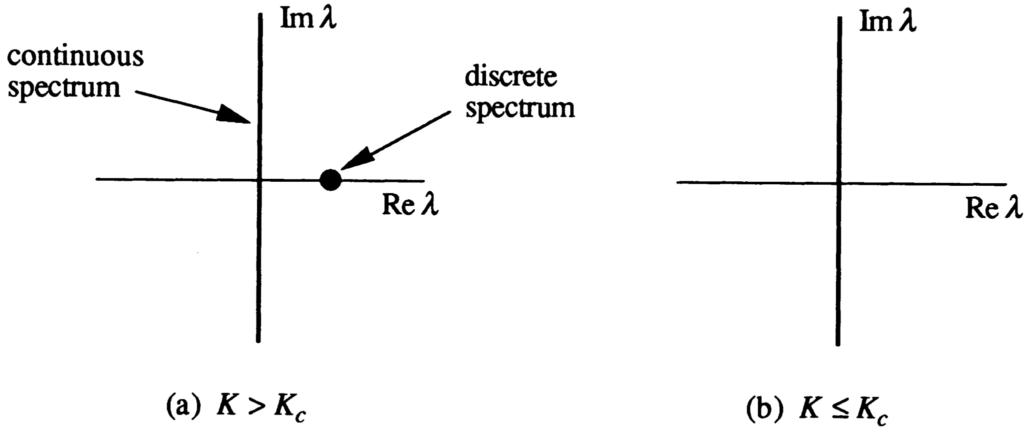
$$\frac{\partial \rho}{\partial t} + \frac{\partial(\rho v)}{\partial \theta} = 0, \tag{8a}$$

where

$$v\,(\theta, t, \omega) = \omega + K \int_{-\pi}^{\pi} \int_{-\infty}^{\infty} \sin(\phi - \theta)\rho(\phi, \nu, t) g(\nu) d\nu d\phi \ . \tag{8b}$$

Equation(8) expresses conservation of oscillators of frequency ω. The velocity v follows from the law of large numbers applied to (1). Seen in this light, we can now say precisely what Kuramoto accomplished: he found the fixed points, i.e., the stationary densities for (8).

Local stability questions can now be addressed by straightforward linearization (Mirollo and Strogatz 1991). Yet when this is done for the incoherent state $\rho_0 \equiv 1/2\pi$, the results are very surprising: ρ_0 is unstable for $K > K_c$, but *neutrally* stable for *all* $0 < K < K_c$. It's odd to find neutral stability for a whole interval of parameters. In the analysis, one encounters spectra like those shown in Fig. 6. Above K_c, there's a continuous spectrum on the imaginary axis, and a single discrete real eigenvalue $\lambda > 0$. As $K \to K_c^+$, λ moves left, gets absorbed in the continuous spectrum, then disappears! Below K_c, the spectrum is purely continuous and imaginary.



(a) $K > K_c$ (b) $K \leq K_c$

Fig. 6. Spectrum for linearization of (8) about the incoherent state ρ_0. (a) $K > K_c$: ρ_0 is unstable, thanks to the discrete eigenvalue $\lambda > 0$. (b) $K \leq K_c$: ρ_0 is neutrally stable.

Even more bizare, numerical integration for $K < K_c$ shows that $r(t)$ decays approximately exponentially at first – despite the fact that there are no negative eigenvalues! This damping can be explained by an analytic continuation argument (Strogatz et. al 1992). It is closely related to "Landau damping", a phenomenon first predicted and later confirmed experimentally in the context of plasma physics (Landau 1946; Infeld and Rowlands 1990). Similar phenomena arise in fields ranging from atomic physics to fluid mechanics – the common feature is the presence of a linear operator with a continuous spectrum (Crawford and Hislop 1989).

From Wiener's brain waves to Landau's plasmas, by way of Winfree's biological rhythms and Kuramoto's statistical mechanics – the analysis of mutual synchronization has revealed some unexpected connections among different branches of science.

4. THE FUTURE

4.1 Needed Experiments

After three decades of research, the study of mutual synchronization is prospering theoretically, but like many branches of mathematical biology, it has wandered too far from its source. There has been no serious confrontation between theory and experiment. We need to follow the example of two related fields: excitable media and central pattern generators. The theory of excitable media has developed alongside experimental work on spiral and scroll waves in the Belousov-Zhabotinsky reaction; see the papers by Tyson (1994) and Winfree (1994) in this volume. Similarly, Ermentrout and Kopell's theory of phase-locking in chains of oscillators (Kopell and Ermentrout 1986; Kopell 1988) has been directly motivated by experiments on the central pattern generator of lamprey, an eel-like creature, and has led to some surprising predictions that were recently verified by their experimental collaborators (Sigvardt et. al 1992).

So what experimental system could be our lamprey? Menstrual synchrony is unpromising; it takes a month for each data point. Circadian rhythms are a bit better, but it's often hard to locate or characterize the individual microscopic oscillators. Fireflies have a much more convenient timescale, but you have to go to Malaysia to measure them. Still, they have many virtues: it's easy to measure the rhythm of an individual firefly over many cycles, and to characterize its mean frequency, cycle-to-cycle variability, response to light pulses, etc. By measuring many individuals separately, one could perhaps estimate the distribution of frequencies and coupling strengths across the population. Most of these remarks apply also to yeast cells, which have the further advantage that they show some experimental indication of phase transitions to and from synchronization as the dilution factor is varied (Aldridge and Pye 1976). Another promising system is the pacemaker organ in the brain of weakly electric fish. This neural oscillator is the most precise biological clock known (Bullock 1970) – it produces a high-frequency sinusoidal oscillation which is as precise as a quartz wristwatch, with a frequency that varies from cycle to cycle by about 1 part in 10^4. Recent experiments suggest that the coupling among the pacemaker cells can be altered by administering appropriate chemicals (Dye 1991).

But I suspect that mutual synchronization is going to be co-opted by physics, where the oscillators are closer to those imagined in our theories. There have already been some exciting applications to charge-density waves (Fisher 1985; Strogatz et. al 1989) and to arrays of microwave oscillators (York and Compton 1991) and superconducting Josephson junctions (Hadley et. al 1988; Tsang et. al 1991; Benz and Burroughs 1991). On second thought, perhaps "co-opted" is not the right word, since mutual synchronization *began* in physics, with Huygens' (1665) discovery of phase-locking between two pendula hung on the same board.

4.2 Theory

Let's now consider the future prospects for the theory of mutual synchronization, and coupled oscillators more generally. There are at least two promising strategies. The first is to study the detailed bifurcation structure of small systems of two or three oscillators, using qualitative methods and numerical bifurcation packages. Recent work in this vein (Aronson et. al 1990) shows that even two coupled oscillators can produce dynamics of bewildering complexity.

The second approach is to study enormously large systems of oscillators, with the aim of focusing on collective behavior. Almost all the existing theoretical work in this area is based on smooth phase-only oscillators coupled in extremely simple ways (all-to-all or in a one-dimensional chain). Relaxing any of these assumptions will lead to new problems.

For example, we know very little about discrete sets of oscillators in two and three dimensions. Pure synchrony is probably rare – we're more likely to find spiral and scroll waves, vortices and defects, new forms of turbulence, and so on. And how is the simple mean-field picture of phase transitions modified in these locally coupled systems? Perhaps renormalization group methods can be extended to such cases. See (Daido 1988; Strogatz and Mirollo 1988) for examples and references.

We should also move beyond the phase model to more complicated kinds of oscillators. Recent work shows that when amplitude variations are permitted, new phenomena arise even in mean-field theory. For instance, the order parameter $r(t)$ can exhibit periodic, quasiperiodic, or chaotic behavior (Matthews and Strogatz 1990; Matthews et. al 1991). This result was obtained for limit-cycle oscillators with weak nonlinearity – in contrast, virtually nothing is known about populations of relaxation oscillators. There are recent indications that they may have superior synchronization properties (Mirollo and Strogatz 1990; Somers and Kopell 1993).

The resetting properties of oscillator populations remain to be explored. Winfree (1980) has discussed populations of independent oscillators all reset by the same stimulus – but what if these oscillators are coupled? A theory here might provide a better understanding of the phase-response curves that are often measured experimentally by circadian biologists.

Finally, how can one use oscillator networks to compute, learn, or recognize patterns? This subject should appeal to people caught up in the current excitement about neural networks. Abbott (1990) has taken a first step in this direction. The recent observation of stimulus-induced synchronization in the visual cortex (Gray et. al 1989) has spawned several theories involving oscillator networks (Singer and Schuster 1991), though there's still uncertainty about the biological significance of the experimental observations (Crick and Koch 1990; Stryker 1989). But in any case, Norbert Wiener would be pleased to see that we're thinking about oscillators in the brain again.

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