SPONTANEOUS SYNCHRONIZATION IN NATURE

Steven H. Strogatz
Department of Theoretical and Applied Mechanics
Kimball Hall
Cornell University
Ithaca, NY 14853

1. Introduction

Mutual synchronization of oscillators is ubiquitous in biology (Winfree 1967, 1980, 1987). Examples include pacemaker cells in the heart (Peskin 1975; Michaels et al. 1987) and nervous system (Dye 1991), 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 now review two of these fascinating examples in some detail.

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 1991).

3. Mathematical Models

3.1 Winfree's Work

In 1967, Art Winfree explored the nonlinear dynamics of 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. 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

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. A peculiar frequency spectrum -- found years earlier by Wiener (1958, 1961) in his studies of the alpha rhythm of brain waves -- pops out of the analysis, as does a formula for the synchronization threshold discussed by Winfree (1967).

3.3 Recent Work

For more recent work on mutual synchronization in biology and physics, see Mirollo and Strogatz (1990), Matthews and Strogatz (1990), Matthews et al. (1991), Strogatz et al. (1992), Strogatz and Stewart (1993), Wiesenfeld et al. (1996), and the references therein.

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