4.5 Fireflies

Fireflies provide one of the most spectacular examples of synchronization in nature. In some parts of southeast Asia, thousands of male fireflies gather in trees at night and flash on and off in unison. Meanwhile the female fireflies cruise overhead, looking for males with a handsome light.

To really appreciate this amazing display, you have to see a movie or videotape of it. A good example is shown in David Attenborough's (1992) television series *The Trials of Life,* in the episode called "Talking to Strangers." See Buck and Buck (1976) for a beautifully written introduction to synchronous fireflies, and Buck (1988) for a more recent review. For mathematical models of synchronous fireflies, see Mirollo and Strogatz (1990) and Ermentrout (1991).

How does the synchrony occur? Certainly the fireflies don't start out synchronized; they arrive in the trees at dusk, and the synchrony builds up gradually as the night goes on. The key is that *the fireflies influence each other*: When one firefly sees the flash of another, it slows down or speeds up so as to flash more nearly in phase on the next cycle.

Hanson (1978) studied this effect experimentally, by periodically flashing a light at a firefly and watching it try to synchronize. For a range of periods close to the firefly's natural period (about 0.9 sec), the firefly was able to match its frequency to the periodic stimulus. In this case, one says that the firefly had been ***entrained*** by the stimulus. However, if the stimulus was too fast or too slow, the firefly could not keep up and entrainment was lost—then a kind of beat phenomenon occurred. But in contrast to the simple beat phenomenon of Section 4.2, the phase difference between stimulus and firefly did not increase uniformly. The phase difference increased slowly during part of the beat cycle, as the firefly struggled in vain to synchronize, and then it increased rapidly through 2π, after which the firefly tried again on the next beat cycle. This process is called *phase walk-through* or ***phase drift.***

Model

Ermentrout and Rinzel (1984) proposed a simple model of the firefly's flashing rhythm and its response to stimuli. Suppose that $\theta(t)$ is the phase of the firefly's flashing rhythm, where $\theta = 0$ corresponds to the instant when a flash is emitted. Assume that in the absence of stimuli, the firefly goes through its cycle at a frequency ω, according to $\dot{\theta} = \omega$.

Now suppose there's a periodic stimulus whose phase Θ satisfies

$$\dot{\Theta} = \Omega, \tag{1}$$

where $\Theta = 0$ corresponds to the flash of the stimulus. We model the firefly's response to this stimulus as follows: If the stimulus is ahead in the cycle, then we assume that the firefly speeds up in an attempt to synchronize. Conversely, the firefly slows down if it's flashing too early. A simple model that incorporates these assumptions is

$$\dot{\theta} = \omega + A\sin(\Theta - \theta) \tag{2}$$

where $A > 0$. For example, if Θ is ahead of θ (i.e., $0 < \Theta - \theta < \pi$) the firefly speeds up ($\dot{\theta} > \omega$). The ***resetting strength*** A measures the firefly's ability to modify its instantaneous frequency.

Analysis

To see whether entrainment can occur, we look at the dynamics of the phase difference $\phi = \Theta - \theta$. Subtracting (2) from (1) yields

$$\dot{\phi} = \dot{\Theta} - \dot{\theta} = \Omega - \omega - A\sin\phi, \tag{3}$$

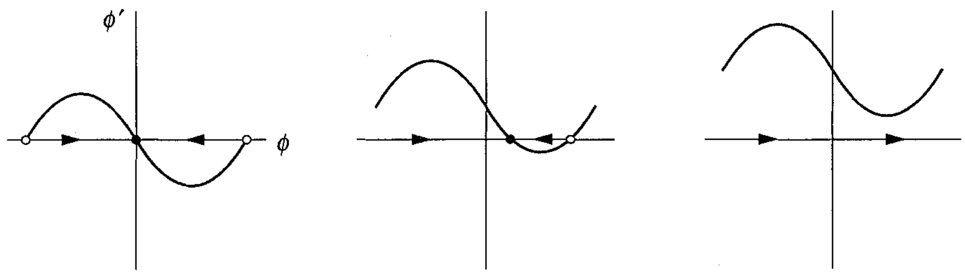
which is a *nonuniform oscillator* equation for $\phi(t)$. Equation (3) can be nondimensionalized by introducing

$$\tau = At, \quad \mu = \frac{\Omega - \omega}{A}. \tag{4}$$

Then

$$\phi' = \mu - \sin\phi \tag{5}$$

where $\phi' = d\phi/d\tau$. The dimensionless group μ is a measure of the frequency difference, relative to the resetting strength. When μ is small, the frequencies are relatively close together and we expect that entrainment should be possible. This is confirmed by Figure 4.5.1, where we plot the vector fields for (5), for different values of $\mu \geq 0$. (The case $\mu < 0$ is similar.)



(a) $\mu = 0$ (b) $0 < \mu < 1$ (c) $\mu > 1$

Figure 4.5.1

When $\mu = 0$, all trajectories flow toward a stable fixed point at $\phi^* = 0$ (Figure 4.5.1a). Thus the firefly eventually entrains with *zero phase difference* in the case $\Omega = \omega$. In other words, the firefly and the stimulus flash *simultaneously* if the firefly is driven at its natural frequency.

Figure 4.5.1b shows that for $0 < \mu < 1$, the curve in Figure 4.5.1a lifts up and the stable and unstable fixed points move closer together. All trajectories are still attracted to a stable fixed point, but now $\phi^* > 0$. Since the phase difference approaches a constant, one says that the firefly's rhythm is ***phase-locked*** to the stimulus.

Phase-locking means that the firefly and the stimulus run with the same instantaneous frequency, although they no longer flash in unison. The result $\phi^* > 0$ implies that the stimulus flashes *ahead* of the firefly in each cycle. This makes sense—we assumed $\mu > 0$, which means that $\Omega > \omega$; the stimulus is inherently faster than the firefly, and drives it faster than it wants to go. Thus the firefly falls behind. But it never gets lapped—it always lags in phase by a constant amount ϕ^*.

If we continue to increase μ, the stable and unstable fixed points eventually coalesce in a saddle-node bifurcation at $\mu = 1$. For $\mu > 1$ both fixed points have disappeared and now phase-locking is lost; the phase difference ϕ increases indefinitely, corresponding to *phase drift* (Figure 4.5.1c). (Of course, once ϕ reaches 2π the oscillators are in phase again.) Notice that the phases don't separate at a uniform rate, in qualitative agreement with the experiments of Hanson (1978): ϕ increases most slowly when it passes under the minimum of the sine wave in Figure 4.5.1c, at $\phi = \pi/2$, and most rapidly when it passes under the maximum at $\phi = -\pi/2$.