Fireflies

Fireflies provide one of the most spectacular examples of synchronization in nature (see e.g. this video here and here). Male fireflies gather on trees and flash on and off in unison at night in order to attract female fireflies.

A simple model of synchronization of fireflies' flashing rhythm in response to stimuli can be given as follows. Let $\theta(t)$ be the phase of the firefly's flashing rhythm, with $\theta = 0$ being the instant when a flash is emitted. Assume that in the absence of external stimuli, the firefly goes through this cycle of on and off at a constant frequency ω, so that $\dot{\theta} = \omega$, where $\dot{\theta} = d\theta/dt$.

Now suppose there exists an external periodic stimulus whose phase Θ satisfies the same differential equation but different frequency Ω, i.e.

$$\dot{\Theta} = \Omega\,, \tag{0.0.1}$$

where $\Omega = 0$ is when the flash of the external stimulus is on. This stimulus can be e.g. another firefly, or even artificial LED light. We can 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 attempt to synchronize.
- Conversely, the firefly tries to slow down if the stimulus is behind (i.e. firefly is flashing too early).

A simple model that incorporates these assumptions is

$$\dot{\theta} = \omega + A\sin(\Theta - \theta)\,, \qquad A > 0\,. \tag{0.0.2}$$

Clearly, if Θ is ahead of θ, i.e. $\Theta - \theta \in (0, \pi)$ then the firefly speeds up ($\dot{\theta} > \omega$). The parameter A is called the *resetting strength* of the firefly, which measures the ability of the firefly to modify its instantaneous frequency.

We say that the firefly has been **entrained** by the stimulus if it successfully matches the frequency of the stimulus.

(a) By defining two dimensionless quantities τ (dimensionless time) and μ, construct a *single* differential equation for a function ϕ that describes the dynamics of synchronization given by the model above.

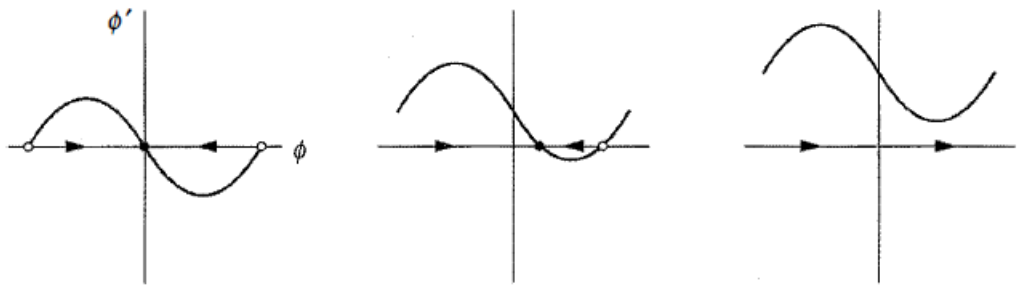
What quantity is ϕ? (**Hint:** two words)

Solution: Note: This is based on Chapter 4 of Strogatz's *Nonlinear Dynamics.* (1 mark) The single variable we are interested in is the *phase difference* $\phi = \Theta - \theta$. Define $\tau = At$ and $\mu = A^{-1}(\Omega - \omega)$. This gives

$$\frac{d\phi}{d\tau} = \mu - \sin\phi\,.$$

(b) Sketch the phase diagram (ϕ', ϕ), where $\phi' = d\phi/d\tau$ for the three cases: (i) $\mu = 0$, (ii) $0 < \mu < 1$, and (iii) $\mu > 1$. On the ϕ-axis of each diagram, draw an arrow to the right if $\phi' > 0$ and to the left when $\phi' < 0$. Hence show that (i) has three fixed points, one of which is stable, (ii) has one stable and one unstable fixed points, while (iii) has no fixed point at all.

Solution: (2 marks) The diagram looks like this:



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

The black dots are stable fixed points and the white ones are unstable.

(c) Use the results so far to argue that for $\mu = 0$ the firefly will eventually flash *simultaneously*.

Solution: (1 mark) From the phase diagram, we see that the stable fixed point is at $\phi_* = 0$. In other words, the long time behaviour is that $\phi \to \phi_* = 0$, hence the stimulus and the firefly have the same phase $\Omega = \omega$. Therefore, they will eventually flash simultaneously at the same instantaneous frequency.

(d) In the similar spirit as part (c), argue that for $\mu \in (0, 1)$ the firefly will be *phase-locked* to the stimulus. Your answer should explain why the term "phase-locking" is used in this regime and the nature of the phase locking itself.

Solution: (1 mark) From the phase diagram, we see that the stable fixed point is at some $\phi_* > 0$. In other words, the long time behaviour is that $\phi \to \phi_* > 0$. Since this value is positive, the stimulus and the firefly will converge towards a fixed constant phase *difference* $\Omega - \omega = \phi_*$. Therefore, although they will not flash at the same time, they will flash with fixed phase lag/advance, with the firefly *lagging* behind the stimulus.

(e) For $\mu > 1$, the firefly is said to be *phase-drifted* relative to the stimulus. However, the phase drift is not uniform. When the phase drift is the fastest and the slowest in terms of the phases of the firefly and the stimulus?

Solution: (1 mark) The phase drift is the fastest and slowest when they are a quarter out of phase, i.e. $\phi = \pm\pi/2$.

(f) The model makes a testable and specific predictions. Show that the **range of entrainment**, which is the range of frequency of the firefly flashing for which it can be entrained, is given by

$$\omega - A \leq \Omega \leq \omega + A\,.$$

The parameter A is typically determined by experiments.

Solution: (2 marks) This follows from considering the fixed point equation for the borderline case $\mu = 1$, since beyond this we know it will phase-drift. Hence we get

$$\sin\phi_* = \frac{\Omega - \omega}{A}\,.$$

Clearly the possible values of ϕ_* for which stable fixed points exist is when $\phi_* \in (-\pi/2, \pi/2)$. Hence $\sin\phi_* \in (-1, 1)$ and we get

$$\omega - A \leq \Omega \leq \omega + A\,.$$

(g) For $\mu > 1$, calculate the period of the phase drift T, which is the time taken for the stimulus and the firefly to flash simultaneously again (but they never synchronize). Hence explain physically why this period is ill-defined or should be regarded as infinity for $\mu \in [0, 1)$.

Solution: (2 marks) By direct integration, we get

$$T = \int dt = \int_0^{2\pi} \frac{dt}{d\phi} d\phi = \int_0^{2\pi} \frac{d\phi}{\Omega - \omega - A\sin\phi} = \frac{2\pi}{\sqrt{(\Omega-\omega)^2 - A^2}}\,.$$

The last equality can be obtained e.g. by substitution $u = \tan(\phi/2)$ or complex integration techniques. This period makes no sense for $\mu \in [0, 1)$ because in those cases they are phase locked with either zero or nonzero phase difference. Therefore, once they are phase locked, the period is effectively infinite (because they *never* phase-drift, or ill-defined (because the denominator is imaginary).