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**Fireflies** (as a practical 'bio' application of the material covered up to this point)

## REFERENCES

- Ermentrout & Rinzel (1984) 'Beyond a pacemaker's entrainment limit: phase walk-through' (American Journal of Physiology)
- Strogatz (1994) 'Nonlinear Dynamics and Chaos' (Chapter 4.5)

## Motivation

- certain southeast Asian fireflies (*Pteroptyx malaccae* for Malaysia in particular) are known to flash in unison rhythmically w/ intervals of 0.4-5 seconds  $\Rightarrow$  synchronization

$\Rightarrow$  show David Attenborough's 'The Trials of Life' (Talking to Strangers)

## QUESTION

- how does this synchronization occur?

(presumably the fireflies arrive in the trees @ night and eventually the synchrony starts to build as the night goes on)

$\Rightarrow$  somehow the fireflies influence one another

each time  $\theta$  passes through here, the firefly flashes

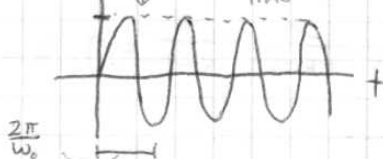
## MODEL

- start with a simple model which describes  $\theta(t)$ , the phase of the firefly's flashing rhythm

- all alone, the firefly goes through the cycle at its own natural frequency, i.e.

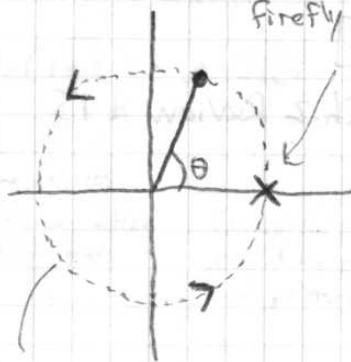
$$\frac{d\theta}{dt} = \omega_0$$

$\sin(\theta)$  firefly flashes each time you hit this line



as time progresses, you go CCW around the circle, thus

$$\theta = \theta(t) \text{ where } 0 \leq \theta \leq 2\pi$$



- a study by Hanson (1978) tried experimentally to understand the basis for this synchronization by periodically flashing a light and watching whether or not the firefly could synchronize or not
- what he found was that there was a specific range of frequencies over which the firefly could synchronize

→ this leads us to formulate a specific question:

### SPECIFIC QUESTION

Can we understand Hanson's result within the context of the simple model?

German for 'time giver'

Assumptions [1] periodic stimulus (zeitgeber) has frequency  $\omega = \frac{2\pi}{T}$

[1] the firefly has the natural (preferred) frequency  $\omega_0 = \frac{2\pi}{T_0}$

\* (NOTE: some fireflies can actually change  $\omega_0$ , see Ermentrout 1991)

[2] however, it can change its firing rate somewhat to match  $\omega$

[1] - if the zeitgeber is ahead of the firefly, it can increase  $\frac{d\phi}{dt}$  and thus fire a bit earlier

[2] - if the zeitgeber is behind the firefly, it can decrease  $\frac{d\phi}{dt}$  and thus fire a bit later

- the amount of increase or decrease on the firefly's part is some smooth function of the phase difference between the two and there is no adjustment when that difference is an integer multiple of  $2\pi$

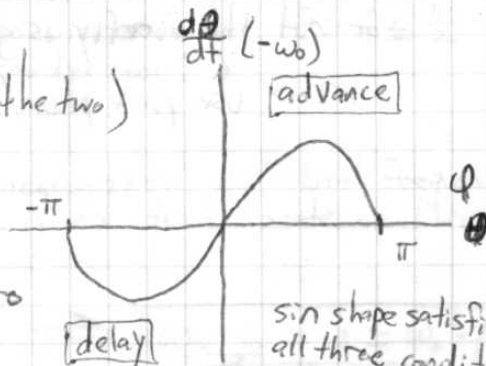
phase of zeitgeber

→ use a sin function

[3] let  $\phi \equiv \omega t - \theta$  (phase difference between the two)

- synchronization occurs when  $\frac{d\phi}{dt} = 0$   
(both flash at the same rate)

- perfect sync. occurs when  $\phi$  and  $\frac{d\phi}{dt}$  are zero  
(both always flash simultaneously)



sin shape satisfies all three conditions in assumption #2

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## Fireflies (cont.)

## Analysis

- pooling our assumption together, we have

$$\frac{d\theta}{dt} = \omega_0 + \beta \sin(\omega t - \theta)$$

where  $\beta$  is the 'coupling strength' (i.e. measure as to how much influence the ability ~~has~~ to synchronize has)

(thought it has units of Hz)

→ a nonlinear, non-autonomous equation

→ can we turn this into an autonomous equation so we can use bifurcation/phase plane analysis?

$$\phi = \omega t - \theta, \text{ so } \frac{d\phi}{dt} = \frac{d}{dt}(\omega t - \theta) = \omega - \frac{d\theta}{dt}$$

diff. between fireflies natural freq. and that of the zeitgeber

$$= \omega - \omega_0 - \beta \sin(\phi) = \frac{d\phi}{dt}$$

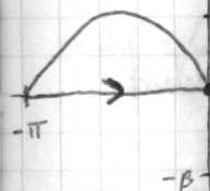
$$\text{now } \omega - \omega_0 = \frac{2\pi}{T} - \frac{2\pi}{T_0} = \frac{2\pi}{TT_0} (T_0 - T) \equiv \delta$$

[thus  $\delta$  tells you about the difference between the fireflies natural frequency and the stimulus driving frequency]

$$\rightarrow \boxed{\frac{d\phi}{dt} = \delta - \beta \sin(\phi)} \quad (\text{still nonlinear, but is autonomous})$$

□ this equation can now be analyzed to provide insight into how/whether or not the firefly is going to be able to synchronize

→ use phase plane/line analysis, considering different case of  $\delta$



□ some perf poss

$\delta > \beta$

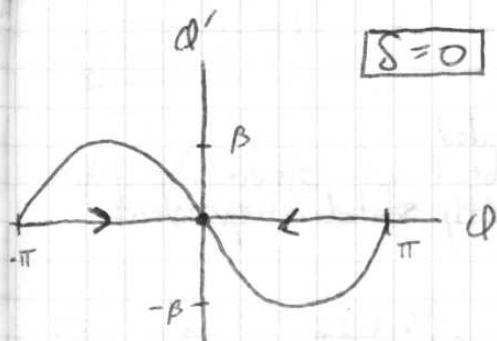
no

→ w

INT

□ our is to sol

Syn



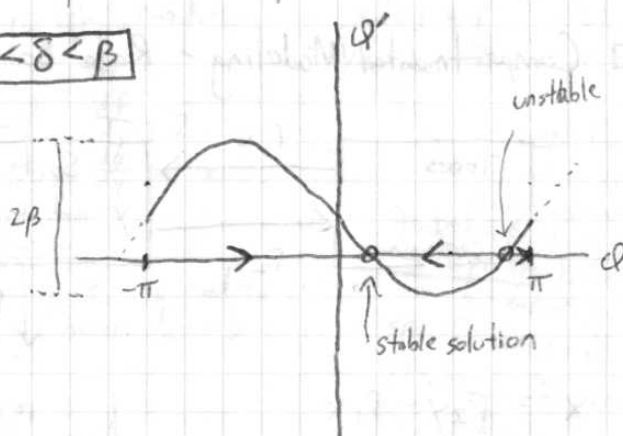
$$\delta = 0$$

$$\phi' = -\beta \sin(\phi)$$

- stable equilibrium at  $\phi = 0$  (perfect synchronization)
- unstable equilibrium at  $\phi = \pm\pi$

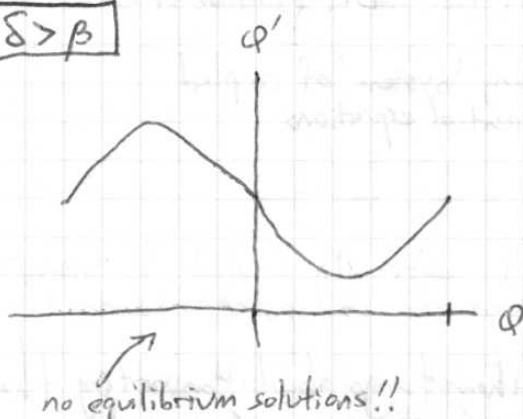
→ firefly will flash in perfect unison w/ stimulus

$$0 < \delta < \beta$$



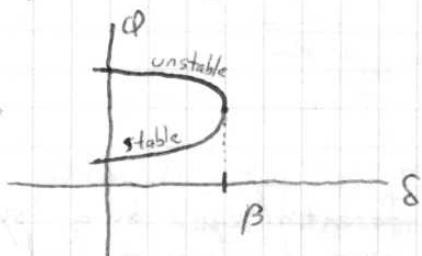
□ somewhat similar picture, but perfect synchrony is no longer possible

$$\delta > \beta$$



□ no equilibria  $\Rightarrow$  synchronization can NOT occur!!

$\Rightarrow$  we thus have a saddle-node bifurcation when  $\delta = \beta$



□ changing  $\beta$  will affect where the bifurcation occurs, so  $\beta$  is effectively a ~~saddle~~ bifurcation parameter as well

□ stable fixed points will occur at  $-\frac{\pi}{2} \leq \phi \leq \frac{\pi}{2}$  (the exact value depending upon  $\delta$ )

### INTERPRETATION

□ our model has explained why the firefly can't synchronize: if its natural frequency is too far from the driving frequency, there is no steady-state equilibrium solution for  $\phi$

synchronization occurs when  $-\beta \leq \delta \leq \beta \Rightarrow \boxed{\omega_0 - \beta \leq \omega \leq \omega_0 + \beta}$

( $\delta = \omega - \omega_0$ ) condition for synchronization (or 'entrainment');

(where the firefly is perpetually trying to catch up/slow down, but can't do it)