§2 Delay models

$$\frac{dN}{dt} = f(N(t))$$

(1) Non-dimensionalise

(2) Find steady states $f(N^*) = 0$

(3) linearise: $N(t) = N^* + n(t)$

small perturbation

$$\frac{dn}{dt} = f'(N^*)\, n(t)$$

$$n(t) = n(0)\, e^{\lambda t}$$

$f'(N^*)$

linear stability requires

$$f'(N^*) < 0$$

Delay model:

$$\frac{dN}{dt} = f(N(t), N(t-T))$$

$T>0$ - delay.

2.1 Delayed logistic model

$$\frac{dN}{dt} = rN(t)\left(1 - \frac{N(t-T)}{K}\right)$$

intrinsic growth rate

carrying capacity

Need to specify $N(t)$ for $-T \le t \le 0$

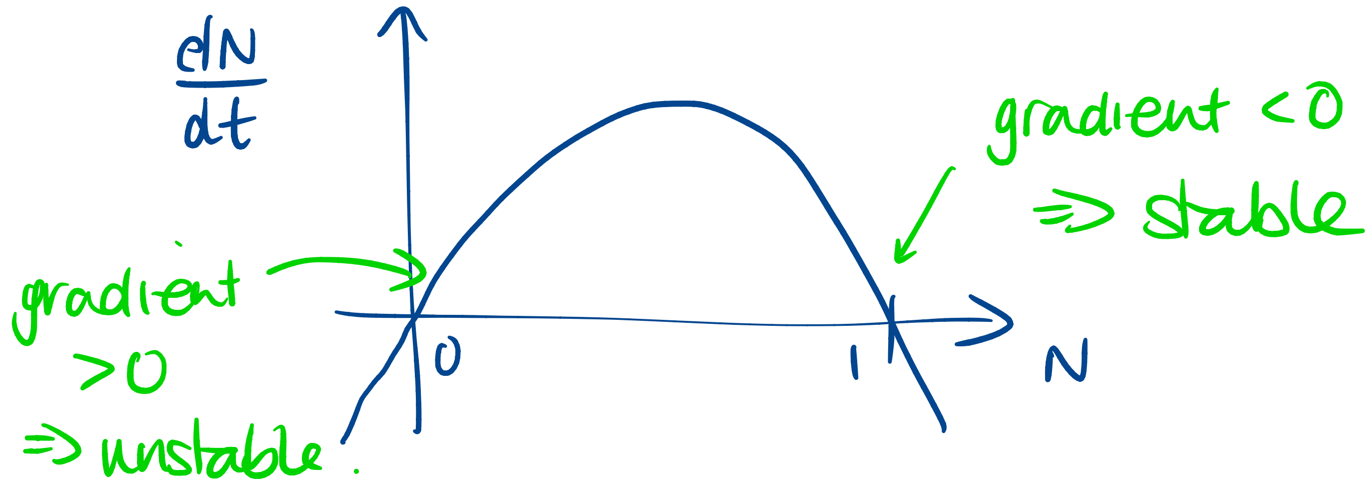
Recall: without a delay $(T=0)$

Non-dimensionalise $\quad N = KN^*$

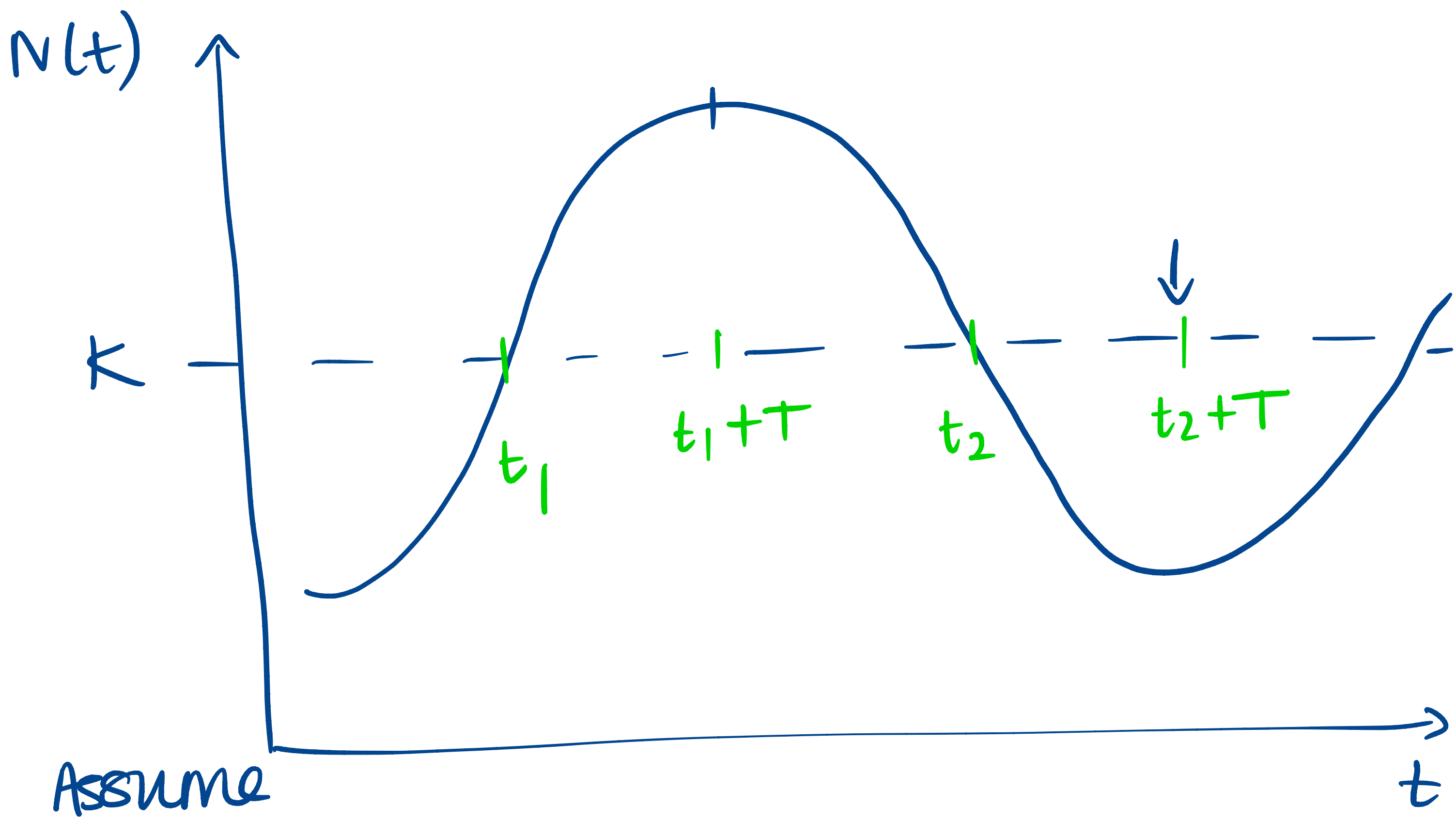
$\quad t^* = rt$

$$\frac{dN}{dt} = N(1-N) \qquad \text{(drop *s)}$$

Steady states: $N^* = 0, 1$



$$\frac{dN}{dt} = rN(t)\left(1 - \frac{N(t-T)}{K}\right)$$



<u>Assume</u>

at $t = t_1$: $N(t_1) = K$.

and for some $t < t_1$, $N(t-T) < K$

$\frac{dN}{dt} > 0$ and so $N(t)$ increasing.

Then, for $t = t_1 + T$, $\frac{dN}{dt} = 0$.

For $t_1 + T < t < t_2$ $\frac{dN}{dt} < 0$

$\Rightarrow$ $N(t)$ is decreasing.

continues until $t = t_2 + T$ when

$\frac{dN}{dt} = 0$ again.

We can observe stable limit cycle solutions for a large range of rT.

If t_p is the period,

$$N(t+t_p) = N(t)$$

NB suppose that the non-delayed model has a periodic solution with period t_p.

$$\int_t^{t+t_p} \left(\frac{dN}{dt'}\right)^2 dt' = \int_t^{t+t_p} f(N)\frac{dN}{dt'}\, dt'$$

$$= \int_t^{t+t_p} f(N)\, dN$$

$$= 0$$

$$\frac{dN}{dt} = 0$$

$\divideontimes$

Non-dimensionalise

$$\frac{dN}{dt} = N(t)\left[1 - N(t-T)\right]$$

Steady states $N^* = 0, 1$

Linearise: $N(t) = 1 + n(t)$

$$\boxed{\frac{dn}{dt} = -n(t-T)}$$

Seek solutions $n(t) = n(0)e^{\lambda t}$

$$\boxed{\lambda = -e^{-\lambda T}}$$

transcendental equation with infinitely many roots.

Want to know if there are values of λ satisfying $\lambda = -e^{-\lambda T}$ s.t. $\mathrm{Re}(\lambda) > 0$.

let $\lambda = \mu + i w$ $\qquad \lambda = -e^{-\lambda T}$

$$\mu + i w = -e^{-(\mu + i w)T}$$

$$\mu = -e^{-\mu T}\cos(wT) \qquad (2.8)$$

$$w = e^{-\mu T}\sin(wT) \qquad (2.9)$$

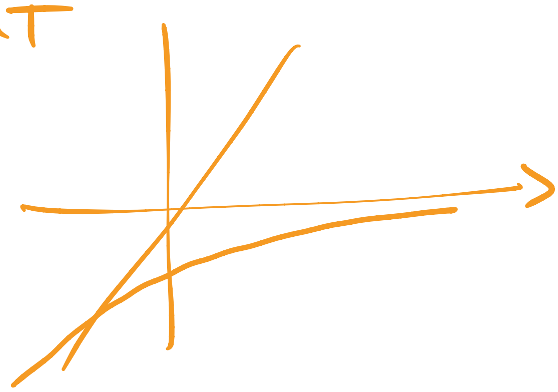
Want to determine the range of values of T for which $\mu < 0$.

- Suppose $w = 0$ $\qquad (2.9)$ ✓✓

  $(2.8) \Rightarrow \mu = -e^{\mu T}$

  No +ve roots

  $\Rightarrow \lambda \in \mathbb{R}$, then linearly stable.



- Suppose $w \neq 0$.

  If w a solution of $(2.8), (2.9)$, so is $-w$.

WLOG consider $w > 0$.

(2.8) $\mu = \underbrace{-e^{-\mu T}} \underbrace{\cos(wT)}$

For $\mu < 0$,

require $0 < wT < \frac{\pi}{2}$

Interested in understanding when, as we increase T, $\mu(T)$ first becomes +ve.

As T increases from zero, then μ first becomes zero when

$wT = \frac{\pi}{2}$.

Eq (2.9) $\Rightarrow$ here $w = 1$

$\Rightarrow$ The steady state first becomes unstable at $T = T_c = \frac{\pi}{2}$ (where $w = 1$).

(For $0 < T < \frac{\pi}{2}$, $N = 1$ is stable).

In dimensional terms,

$N(t) = K$ is a stable steady state

if $\quad 0 < rT < \frac{\pi}{2}$.

2.2 Cheyne-Stokes respiration

Breath volume (ventilation), $V(t)$

$$V(t) = V_{max} \cdot \frac{C^m(t-t_0)}{A^m + C^m(t-t_0)}$$

max ventilation

levels of aerterial CO_2

$A > 0$
$m > 0$ } determined from exp. data.

Production removal

$$\frac{dC}{dt} = P - B\,C(t)\,V(t)$$

$$= P - B\,C(t)\,V_{max} \frac{C^m(t-t_0)}{A^m + C^m(t-t_0)}$$

specify ICs : $C(t)$ for $-t_0 \leq t \leq 0$

$$\frac{dc}{dt} = P - BV_{max}\, C(t) \cdot \frac{C^m(t-t_0)}{A^m + C^m(t-t_0)}$$

$$C(t) = A\, c(\tau) \qquad t = \frac{A}{P}\tau, \quad t_0 = \frac{A}{P}\tau_0$$

$$V(t) = V_{max}\, v(\tau)$$

$$\frac{d}{dt} = \frac{d\tau}{dt} \cdot \frac{d}{d\tau} = \frac{P}{A}\frac{d}{d\tau}$$

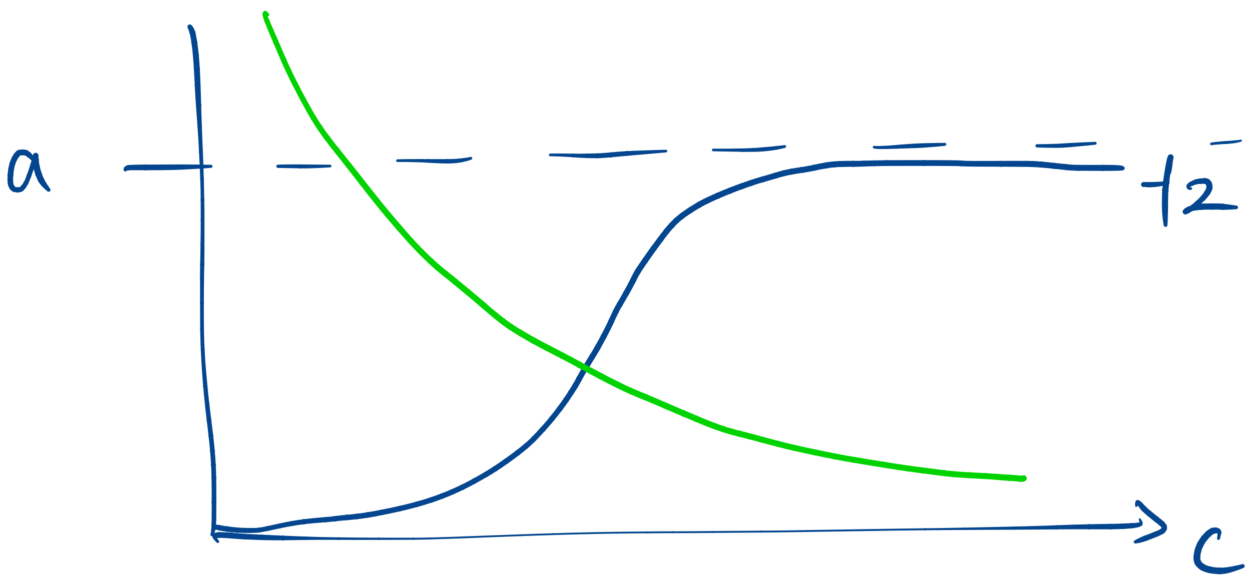
$$\frac{\cancel{A}\,\cancel{P}}{\cancel{A}} \frac{dc}{d\tau} = \cancel{P}^{\,1} - \frac{BV_{max} A\, c(\tau)}{P} \cdot \frac{\cancel{A^m}\, c^m(\tau-\tau_0)}{1\,\cancel{A^m} + \cancel{A^m} c^m(\tau-\tau_0)}$$

$$\frac{dc}{d\tau} = 1 - a\, c(\tau)\, v(\tau)$$

$$= 1 - a\, c(\tau) \cdot \frac{c^m(\tau-\tau_0)}{1 + c^m(\tau-\tau_0)}$$

$$a = \frac{ABV_{max}}{P}$$

Steady States : $\dfrac{1}{c^*} = a\, v(c^*) = \dfrac{a\, c^{*m}}{1 + c^{*m}}$



$$f_1(c) = \frac{1}{c}$$

$$f_2(c) = \frac{ac^m}{1+c^m}$$

$\Rightarrow$ a unique steady state

linear stability analysis

$$V_* = \frac{C_*^m}{1+C_*^m}$$

and let $C(\tau) = C_* + \varepsilon c_1(\tau) + \dots$

$$V(c) = V(C_* + \varepsilon c_1(\tau) + \dots)$$

$$= V_* + \varepsilon V'(C_*) c_1(\tau - \tau_0) + \dots$$

$$v'(c_*) = \left.\frac{dv}{dc}\right|_{c=c^*}$$

$v'(c_*) > 0$

(sketch).

$$\frac{dc}{d\tau} = 1 - a\,c(\tau)\,v(\tau)$$

$$= 1 - a\,c(\tau)\,\frac{c^m(\tau-\tau_0)}{1+c^m(\tau-\tau_0)}$$

$$\varepsilon\frac{dc_1}{d\tau} = 1 - a\left(c_* + \varepsilon c_1 + \dots\right) \times \left(v_* + \varepsilon v'(c_*)\,c_1(\tau-\tau_0) + \dots\right)$$

$$\frac{dc_1}{d\tau} = -a\,v_*\,c_1(\tau) - a\,c_*\,v'(c_*)\,c_1(\tau-\tau_0)$$

$\cancel{+\text{h.o.t.}}$

Seek solutions: $c_1(\tau) = c_1(0)\,e^{\lambda\tau}$

$$\boxed{\lambda = -a\left[v_* + c_*\,v'(c_*)\,e^{-\lambda\tau_0}\right]}$$

$$\boxed{\lambda = -a\left[v_* + c_* v'(c_*) e^{-\lambda \tau_0}\right]}$$

For no delay : $\tau_0 = 0$

$$\lambda = -a\left[v_* + c_* v'(c_*)\right] < 0$$

✓✓ Stable.

For $\forall \lambda \in \mathbb{R}$, $\lambda < 0$ $\Rightarrow$ linearly stable

Now suppose $\lambda = \mu + i w$ $(w \neq 0)$

$$\mu + i w = -a\left[v_* + c_* v'(c_*) e^{-(\mu + i w)\tau_0}\right]$$

$$\mu = -a\left[v_* + c_* v' c_* \right) e^{-\mu \tau_0} \cos(w \tau_0)]$$

$$= -\alpha - \beta e^{-\mu \tau_0} \cos(w \tau_0)$$

$$w = a c_* v'(c_*) e^{-\mu \tau_0} \sin(w \tau_0)$$

$$= \beta e^{-\mu \tau_0} \sin(w \tau_0)$$

$\alpha = a v_* > 0$

$\beta = a c_* v'(c_*) > 0$.

$$\mu = -\alpha - \beta e^{-\mu \tau_0} \cos(w\tau_0)$$

Bifurcation to oscillating solutions at $\mu = 0$:

$$\cos(w\tau_0) = -\frac{\alpha}{\beta} \quad (2.28)$$

$$\sin(w\tau_0) = \frac{w}{\beta} \quad (2.29)$$

$$\Rightarrow \quad w^2 = \beta^2 - \alpha^2 \quad (2.30)$$

(2.28): infinite roots for $\alpha < \beta$

consider the smallest of these (in abs value)

For a bifurcation at $\tau_0 = \tau_0^*$

$$w\tau_0^* = \pi - \cos^{-1}\left(\frac{\alpha}{\beta}\right)$$

$$w^2 = \beta^2 - \alpha^2$$

$$\Rightarrow \quad \tau_0^* = \frac{\pi - \cos^{-1}\left(\frac{\alpha}{\beta}\right)}{\sqrt{\beta^2 - \alpha^2}}$$

2.2.2 Physiologically relevant parameters

$$V_* = V(C_*) = V_{max} \frac{C_*^m}{A^m + C_*^m}$$

$C_* = 40 \text{ mmHg}$, $P = 6 \text{ mmHg min}^{-1}$

$t_0 = 0.25 \text{ min}$, $V_* = 7 \text{ L min}^{-1}$

$V'(C_*) = 4 \text{ L min}^{-1} \text{ mmHg}^{-1}$

$$B = \frac{P}{C_* V_*} \approx 0.021 \text{ L}^{-1} \text{ min}^{-1}$$

$$\omega \tau_0 = \pi - \cos^{-1}\left(\frac{\alpha}{\beta}\right)$$

aV_*

$a C_* V'(C_*)$

$$= \pi - \cos^{-1}\left(\frac{V_*}{C_* V'(C_*)}\right)$$

$$= \pi - \cos^{-1}\left(\frac{7}{4 \times 40}\right)$$

$$\approx \frac{\pi}{2}$$

$$\alpha = a v_* = a\, v(c_*) = \frac{AB}{P} v_*$$

$$\beta = c_* v'(c_*) = \frac{AB}{P} c_* v'(c_*)$$

For stability

$$T_0 < \frac{\boxed{\pi - \cos^{-1}\left(\frac{\alpha}{\beta}\right)}}{\sqrt{\beta^2 - \alpha^2}} \quad \approx \pi/2$$

$$\frac{\cancel{P} t_0}{\cancel{A}} \left\{ \left(\frac{\cancel{A}B}{\cancel{P}}\right)^2 \left[c_*^2 v'(c_*)^2 - v_*^2\right] \right\}^{\frac{1}{2}} \lesssim \frac{\pi}{2}$$

Recall : $P - B c_* v_* = 0$ (defn of st. 87)

$$B t_0 \left(\underbrace{\frac{1}{v_*^2} v'(c_*)^2}_{\text{dominates}} - \underbrace{\frac{1}{c_*^2}}_{} \right)^{\frac{1}{2}} \lesssim \frac{\pi}{2}$$

dominates

$$V'(C_*) \lessapprox \frac{\pi V_*}{2Pt_0}$$

(condition for stability)

Non-dimensional period

$$= \frac{2\pi}{w} \approx 4T_0$$

$$\left(wT_0 \approx \frac{\pi}{2}\right)$$

In dimesional terms:

$$\text{period} \approx 4t_0 \approx 1\,\text{min}$$
