MP problem set 3 answers



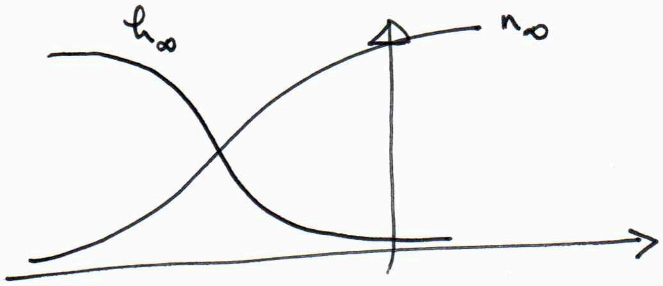
1/ $\varepsilon \ll 1 \ll \gamma$

(i) So $V$ is fast $\rightarrow$ $V$ nullcline $h \simeq h_0(V)$

$h$ intermediate so $h \rightarrow h_\infty(V)$ $(= h_0(V))$ $\Rightarrow$ $V, h$ (fixed point)

$n$ slow $n \rightarrow n_\infty(V)$

(ii)



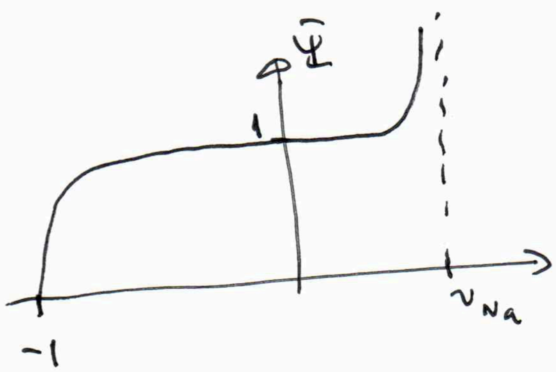

$$h_0(V) = (1+\lambda)\,\Phi(V)\, n_\infty(V)$$

$$\Phi = \frac{1 - e^{-(V+1)/\delta}}{1 - e^{-(v_{Na}-V)/\delta}}$$

For $-1 < V < v_{Na}$, exponentials are small so $\Phi \simeq 1$.

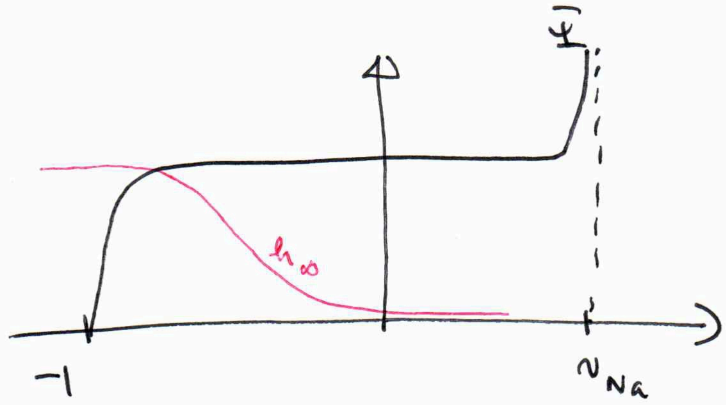
near $v_{Na}$ as $V \rightarrow v_{Na}$ $\Phi \rightarrow \infty$ over $v_{Na} - V \sim \delta$

as $V \rightarrow -1$ $\Phi \rightarrow 0$ over $1 + V \sim \delta$

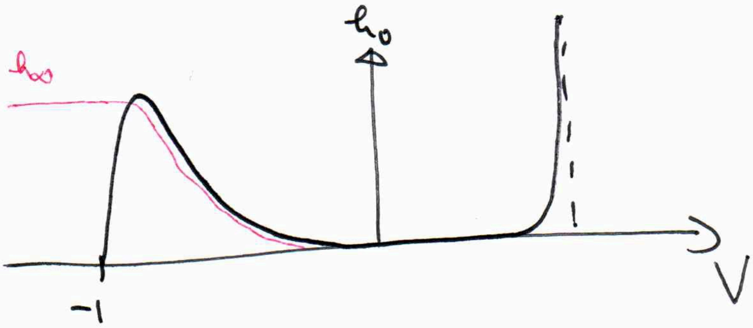


(iii)

so $h_0(V) = (1+\lambda)\,\Phi(V)\,h_\infty(V)$




$\Downarrow$




At the fixed point $h_0 = h_\infty$

so $(1+\lambda)\,\Phi(V) = 1$ $\quad$ $\Phi$ is m.i. so unique

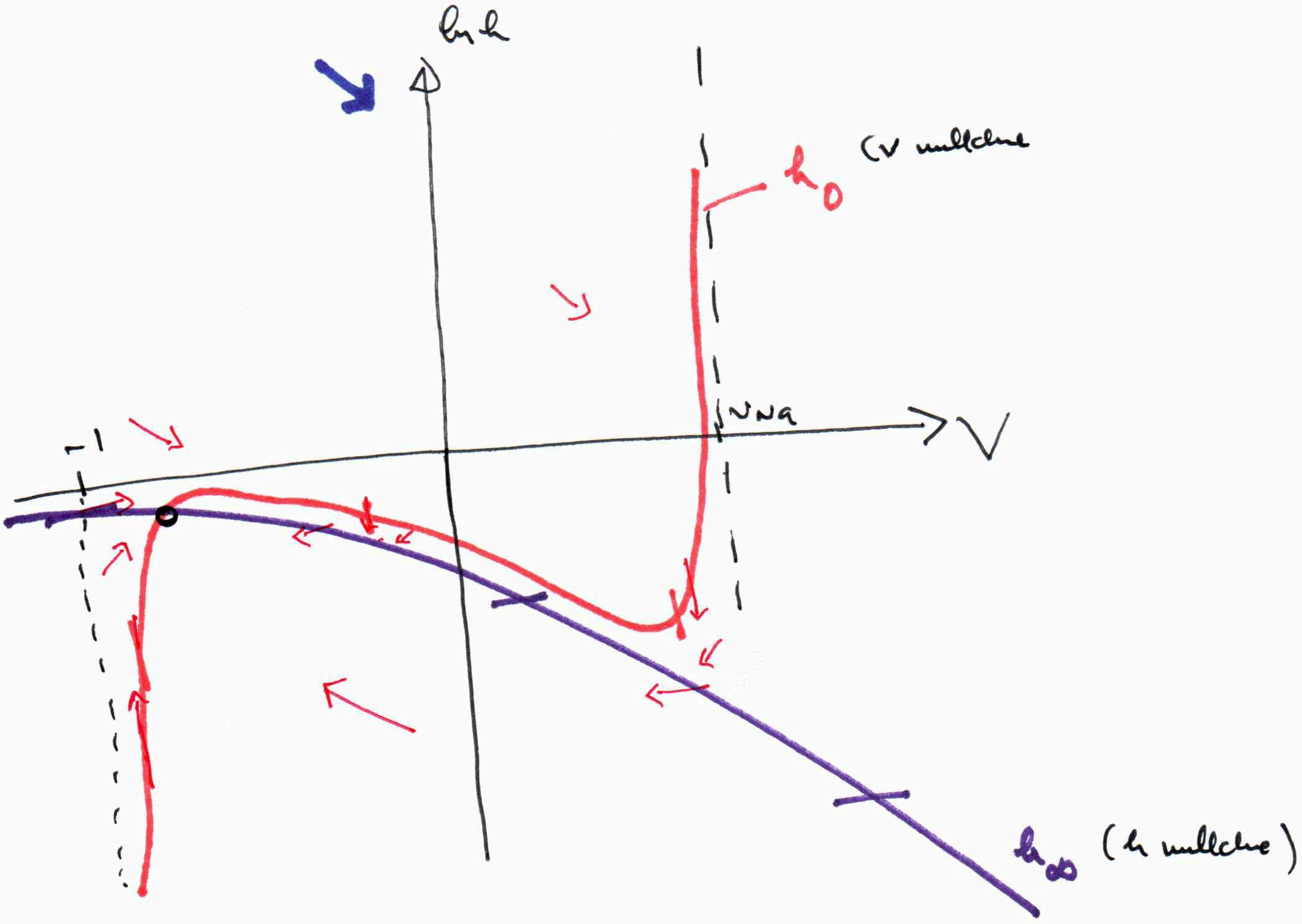
$\lambda \ll 1$ so $\Phi \lesssim 1$ near $V=-1$

approx $(1+\lambda)\left(1-e^{-(V+1)/\delta}\right) \approx 1$

$\Rightarrow \quad e^{-(V+1)/\delta} = 1 - \frac{1}{1+\lambda} \approx \lambda$

$$V \simeq -1 + \delta \ln \frac{1}{\lambda}$$

To visualise phase plane, use $\ln h$ as vertical axis




i nullclines

ii direction large $h$ $\dot V > 0$ $\dot h < 0$

iii fill in other directions

iv clearly trajectories cycle round fixed pt $\Rightarrow$ not a saddle

$\rightarrow$ stability if $\mathrm{tr}\, M < 0$, $M = \begin{pmatrix} -1 & h_0' \\ \gamma & -\gamma h_0' \end{pmatrix}$ (on $\begin{pmatrix} h \\ V \end{pmatrix}$)

$\mathrm{tr} M = -1 - \gamma h_0'$, $\gamma \gg 1$

So stable if $h_0' > 0$

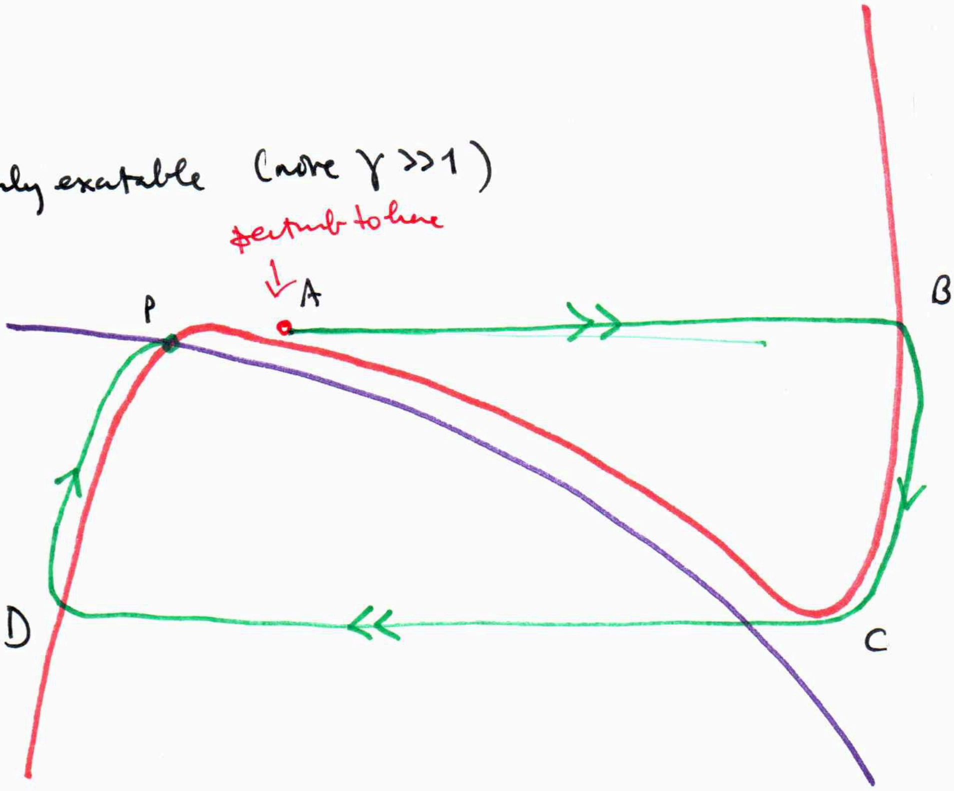
At the fixed pt: $V+1 = \delta \ln \frac{1}{\lambda}$ so $e^{-(V+1)/\delta} = \lambda$

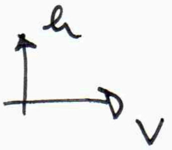
$$h_0' \approx \left\{\left[1 - e^{-(V+1)/\delta}\right] h_\infty\right\}' = (1-\lambda) h_\infty' + \frac{1}{\delta} e^{-(V+1)/\delta} h_\infty$$

$$\approx h_\infty' + \frac{\lambda}{\delta} h_\infty > 0$$

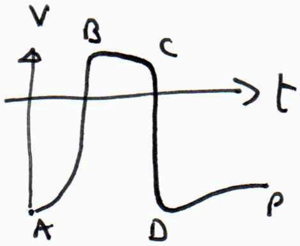
provided $\frac{\lambda}{\delta} > \frac{|h_\infty'|}{h_\infty}$ ($\simeq 0$ anyway)

Clearly excitable (note $\gamma \gg 1$)



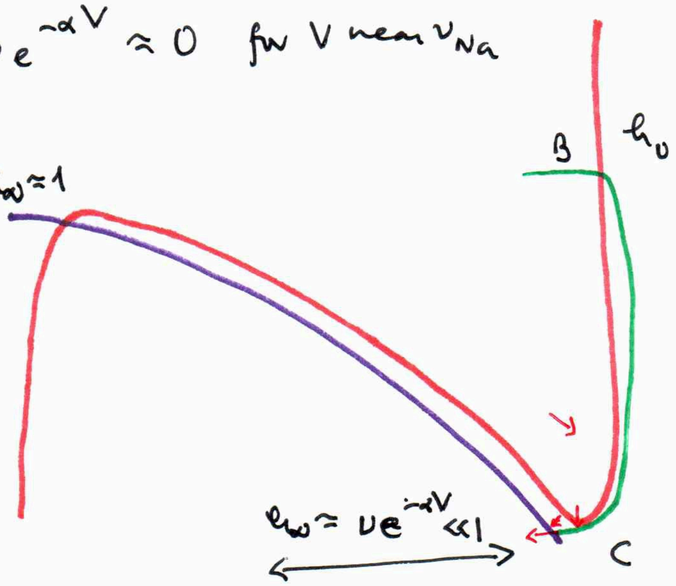

Action potential




(iv) Now $h_\infty \approx 1$ near $V = -1$

$h_\infty \approx \nu e^{-\alpha V} \approx 0$ for $V$ near $v_{Na}$

Now

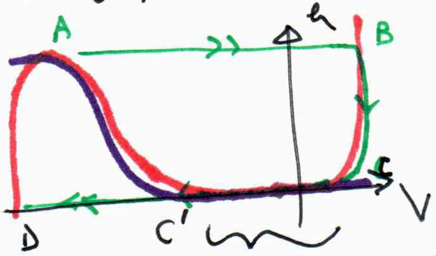



$\dot{h} = h_\infty(V) - h$

$\dot{V} = \gamma[h - h_0(V)]$

$h_\infty \approx \nu e^{-\alpha V} \ll 1$

~~For V near $v_{Na}$ with $h \approx h_0$, we have~~ or in ordinary $h$ variable




The basic idea is the progression from C to C' is slow.

It's not too obvious what the inequalities are for.

Here it is

(a) we want the minimum of $h_0$ to be beyond the $\delta$ ~~the~~ neighborhood of $v_{Na}$.

$$h_0 \simeq \frac{1+\lambda}{1-e^{-(v_{Na}-V)/\delta}} \, \nu e^{-\alpha V}$$

write $V = v_{Na} - w$

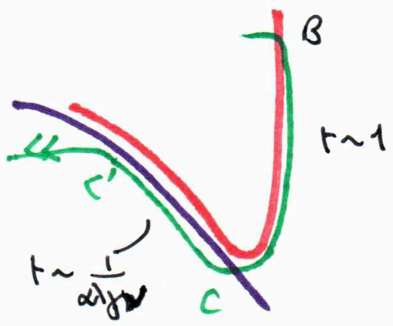
$$\frac{1}{h_0}\frac{dh_0}{dV} = -\frac{d}{dw}\left[\ln\left\{\frac{e^{\alpha w}}{1-e^{-w/\delta}}\right\}\right]$$

$$\propto \; -\alpha\delta + \frac{e^{-w/\delta}}{1-e^{-w/\delta}}$$

so if $\delta\alpha \ll 1$ then the minimum is in $w \gg \delta$ & thus take $\Phi \simeq 1$ there.

(b) Time to get along $CC'$.

$$\dot h = h_\infty - h$$
$$\dot V = \gamma[h-(1+\lambda)h_\infty]$$




so $h$ stays close to $h_\infty$

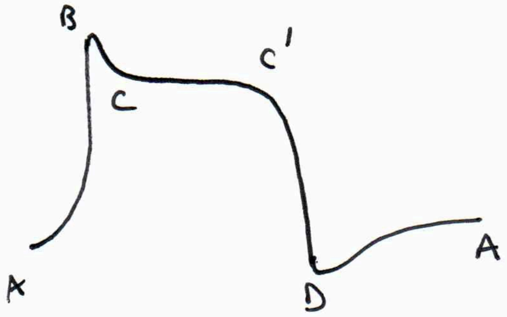
and thus $\dot V \simeq -\gamma\lambda h_\infty = -\gamma\lambda\nu e^{-\alpha V}$

so $\dot{\left(e^{\alpha V}\right)} \simeq -\alpha\lambda\gamma\nu$ ; if $\alpha\lambda\gamma\nu \ll 1$ this phase is longer than $BC$

and the time for $V$ to get from $v_{Na}$ ~~δ~~ $(\sim C)$ to $-\frac{1}{\alpha}\ln\frac{1}{\nu}$ $(\sim C')$

i.e. $e^{\alpha V}$ from $e^{\alpha v_{Na}}$ to $\nu$ is $\sim \dfrac{e^{\alpha v_{Na}}}{\alpha\lambda\gamma\nu}$

Resulting action potential is then




If $\lambda$ depends on $n$: well, various choices here. Suppose the equilibrium $P$ is an exact equilibrium ie $n = n_\infty(V)$ gives orange curve.

~~suppose $\lambda$ increases with $n$~~

If $\lambda \uparrow n$

on excursion $\lambda$ slowly increases (as $n_\infty$ increases), pulls $h_0$ up, no alteration really.

If $\lambda \downarrow n$

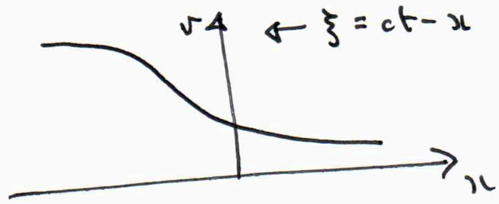
Depends on size of $\lambda$ & $\varepsilon$. If $\varepsilon \ll \lambda$, no real change

but if $\lambda < \varepsilon$, then during the excursion BC $(t \sim 1)$

$h_0$ can be pulled down below $h_\infty$:


There is then a quasi-steady stable state for $h$, V; n continues to increase, pulls $h_0$ down further and the steady state remains unless it becomes unstable which seems unlikely → bistability.

$$v_t = f(v) + \nabla^2 v$$




$v = V(\xi)$, $\xi = ct - x$

$$cV' = V'' + f(V)$$

$$v = V\left[\psi(\underset{\sim}{x}, t)\right]$$

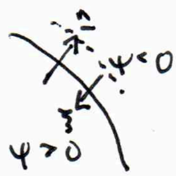
$$v_t = V'\psi_t \qquad (V' = V'(\psi))$$

$$\underset{\sim}{\nabla} v = V' \underset{\sim}{\nabla}\psi$$

$$\nabla^2 v = V''|\underset{\sim}{\nabla}\psi|^2 + V'\nabla^2\psi$$

so $$V'\psi_t = f(v) + V''|\underset{\sim}{\nabla}\psi|^2 + V'\nabla^2\psi$$

$$\Rightarrow V'(\psi_t - \nabla^2\psi) = f(v) + V''|\underset{\sim}{\nabla}\psi|^2$$




$$\delta\psi = \underset{\sim}{\nabla}\psi \cdot \delta\underset{\sim}{x} = \frac{\underset{\sim}{\nabla}\psi}{|\underset{\sim}{\nabla}\psi|}\,|\underset{\sim}{\nabla}\psi| \cdot \delta\underset{\sim}{x} = -\underset{\sim}{n}\cdot\delta\underset{\sim}{x}\,|\underset{\sim}{\nabla}\psi| = \delta\xi\,|\underset{\sim}{\nabla}\psi|$$

so $$\frac{\partial\psi}{\partial\xi} = |\underset{\sim}{\nabla}\psi| \qquad \left(\underset{\sim}{n} = -\frac{\underset{\sim}{\nabla}\psi}{|\underset{\sim}{\nabla}\psi|}\right)$$

The front velocity $\underset{\sim}{v}$ satisfies $\psi_t + \underset{\sim}{v}\cdot\underset{\sim}{\nabla}\psi = 0$

so $$\frac{\psi_t}{|\underset{\sim}{\nabla}\psi|} = -\frac{\underset{\sim}{\nabla}\psi}{|\underset{\sim}{\nabla}\psi|}\cdot\underset{\sim}{v} = \underset{\sim}{v}\cdot\underset{\sim}{n} = v_n$$

$$\underline{\nabla}\cdot\underline{n} = \underline{\nabla}\cdot\left[\frac{-\underline{\nabla}\psi}{|\underline{\nabla}\psi|}\right]$$

$$= -\frac{\nabla^2\psi}{|\underline{\nabla}\psi|} - \underline{\nabla}\psi\cdot\underline{\nabla}\left(\frac{1}{|\underline{\nabla}\psi|}\right)$$

$$= -\frac{\nabla^2\psi}{|\underline{\nabla}\psi|} - \underline{\nabla}\psi\cdot\left(-\frac{1}{|\underline{\nabla}\psi|^2}\underline{\nabla}|\underline{\nabla}\psi|\right)$$

$$= -\frac{\nabla^2\psi}{|\underline{\nabla}\psi|} + \frac{\underline{\nabla}\psi}{|\underline{\nabla}\psi|}\cdot\frac{\underline{\nabla}|\underline{\nabla}\psi|}{|\underline{\nabla}\psi|}$$

$$= -\frac{1}{|\underline{\nabla}\psi|}\left(\nabla^2\psi + \underline{n}\cdot\underline{\nabla}|\underline{\nabla}\psi|\right)$$

$$= -\frac{1}{|\underline{\nabla}\psi|}\left(\nabla^2\psi + \frac{\partial}{\partial n}|\underline{\nabla}\psi|\right)$$

note sign

$$\left\{= -\frac{1}{|\underline{\nabla}\psi|}\left(\nabla^2\psi - \frac{\partial}{\partial\xi}|\underline{\nabla}\psi|\right)\right.$$

Now in terms of the coordinate $\xi$

$$\frac{\partial V}{\partial\xi} \approx V'\frac{\partial\psi}{\partial\xi} = V'|\underline{\nabla}\psi|$$

&

$$\frac{\partial^2 V}{\partial\xi^2} \approx V''|\underline{\nabla}\psi|^2 + V'\frac{\partial}{\partial\xi}|\underline{\nabla}\psi|$$

So

$$V'(\psi_t - \nabla^2\psi) = f(V) + V''|\underline{\nabla}\psi|^2$$

$$= f(V) + V_{\xi\xi} - V'\frac{\partial}{\partial\xi}|\underline{\nabla}\psi|$$

$$\Rightarrow \frac{1}{|\underline{\nabla}\psi|}V_\xi\left(\psi_t - \nabla^2\psi + \frac{\partial}{\partial\xi}|\underline{\nabla}\psi|\right) = f(V) + V_{\xi\xi}$$

which has a solution providing $\psi_t - \nabla^2\psi + \frac{\partial}{\partial\xi}|\underline{\nabla}\psi| = c|\underline{\nabla}\psi|$

or using above results $\quad \dfrac{\psi_t}{|\underline{\nabla}\psi|} = \dfrac{1}{|\underline{\nabla}\psi|}\left(\nabla^2\psi - \dfrac{\partial}{\partial\xi}|\underline{\nabla}\psi|\right) + c$

i.e. $\underline{v_n = c - \underline{\nabla}\cdot\underline{n}}$ $\quad$ (note $\frac{\partial}{\partial n} = -\frac{\partial}{\partial\xi}$)

Target wave

sign

We need to take $\psi = ct - f(r)$, $f' > 0$
for outgoing wave
so $\psi_r < 0$

$\nabla\psi = (-f', 0)$

$|\nabla\psi| = f'$

$$v_n = \frac{\psi_t}{|\nabla\psi|} = \frac{c}{f'}$$

$\underset{\sim}{n} = \hat{\underset{\sim}{r}}$ outward normal

so $\underline{\nabla}.\underline{n} = \frac{1}{r}\frac{\partial}{\partial r}(r) = \frac{1}{r}$

So $\frac{c}{f'} = c - \frac{1}{r}$

and $f' = \frac{c}{c - \frac{1}{r}} = \frac{cr}{cr-1} = 1 + \frac{1}{cr-1}$

$\Rightarrow f = r + \frac{1}{c}\ln(rc-1)$

$\Rightarrow \psi = ct - r - \frac{1}{c}\ln(cr-1)$ for $r > \frac{1}{c}$

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$$\psi = R(\theta,t) - r$$

$$\Rightarrow \psi_t = R_t$$

$$\underline{\nabla}\psi = \left(\psi_r, \frac{1}{r}\psi_\theta\right) = \left(-1, \frac{R_\theta}{r}\right)$$

so $$|\underline{\nabla}\psi| = \left(1 + \frac{R_\theta^2}{r^2}\right)^{1/2}$$

$$\Rightarrow (r=R) \quad v_n = \frac{R_t}{\left(1+\frac{R_\theta^2}{R^2}\right)^{1/2}} = \frac{RR_t}{(R^2+R_\theta^2)^{1/2}}$$

$$\underline{n} = \frac{\left(1, -\frac{R_\theta}{r}\right)}{\left(1+\frac{R_\theta^2}{r^2}\right)^{1/2}}$$

$$\underline{\nabla}\cdot\underline{n} = \frac{1}{r}\frac{\partial}{\partial r}\left[r \cdot \frac{1}{\left(1+\frac{R_\theta^2}{r^2}\right)^{1/2}}\right] + \frac{1}{r}\frac{\partial}{\partial\theta}\left[\frac{-R_\theta}{r\left(1+\frac{R_\theta^2}{r^2}\right)^{1/2}}\right]$$

$$= \frac{1}{r}\frac{\partial}{\partial r}\left[\frac{r^2}{(r^2+R_\theta^2)^{1/2}}\right] - \frac{1}{r}\frac{\partial}{\partial\theta}\left[\frac{R_\theta}{(r^2+R_\theta^2)^{1/2}}\right]$$

$$= \frac{1}{r}\left[\frac{2r}{(r^2+R_\theta^2)^{1/2}} - \frac{r^2 \cdot r}{(r^2+R_\theta^2)^{3/2}}\right] - \frac{1}{r}\left[\frac{R_{\theta\theta}}{(r^2+R_\theta^2)^{1/2}} - \frac{R_\theta^2 R_{\theta\theta}}{(r^2+R_\theta^2)^{3/2}}\right]$$

$$= \frac{r\{2(r^2+R_\theta^2) - r^2\} - \{R_{\theta\theta}(r^2+R_\theta^2) - R_\theta^2 R_{\theta\theta}\}}{r(r^2+R_\theta^2)^{3/2}}$$

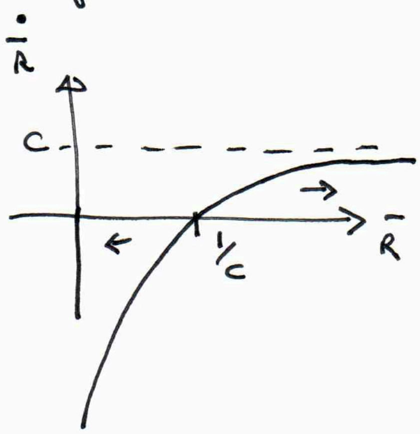
and putting $r=R$, $$\underline{\nabla}\cdot\underline{n} = \frac{R(R^2+2R_\theta^2) - R^2 R_{\theta\theta}}{R(R^2+R_\theta^2)^{3/2}}$$

so

$$\frac{RR_t}{(R^2+R_\theta^2)^{1/2}} = c - \frac{R(R^2+2R_\theta^2) - R R_{\theta\theta}}{(R^2+R_\theta^2)^{3/2}}$$

$$\Rightarrow \quad R_t = \frac{c(R^2+R_\theta^2)^{1/2}}{R} - \frac{\{R^2+2R_\theta^2 - RR_{\theta\theta}\}}{R(R^2+R_\theta^2)} \qquad \square$$

(i) $R=\bar R(t)$ if $\quad \dot{\bar R} = c - \frac{1}{\bar R}$ (and can solve..)




If $\bar R(0) > \frac{1}{c}$, then $\bar R \to \infty$,

$\bar R \sim ct$

If $\bar R(0) < \frac{1}{c}$ $\quad \bar R \to 0 \to$ no spread.

(ii) $R = \bar R + \rho$

$$\Rightarrow \quad c - \frac{1}{\bar R} + \rho_t = c\left[1+\frac{\rho_\theta^2}{(\bar R+\rho)^2}\right]^{1/2} - \frac{\left\{1 - \frac{\rho_{\theta\theta}}{\bar R+\rho} + 2\left(\frac{\rho_\theta}{\bar R+\rho}\right)^2\right\}}{(\bar R+\rho)\left[1+\frac{\rho_\theta^2}{(\bar R+\rho)^2}\right]}$$

linearise: $\rho$ small

$$\Rightarrow \quad c - \frac{1}{\bar R} + \rho_t = c - \frac{\left[1 - \frac{\rho_{\theta\theta}}{\bar R} \dots\right]\left(1 - \frac{\rho}{\bar R} \dots\right)}{\bar R}$$

$$= c - \frac{1}{\bar R}\left(1 - \frac{\rho_{\theta\theta}}{\bar R} - \frac{\rho}{\bar R} \dots\right)$$

(3

So $\rho_t \approx \frac{1}{\bar{R}^2}(\rho_{\theta\theta} + \rho)$

~~This has solution~~ ~~$\rho \propto \exp[\sigma t$~~

Define $\tau = \int_0^t \bar{R}^{-2}\,dt$

$\Rightarrow \rho_\tau = \rho_{\theta\theta} + \rho$

Solutions $\rho = \exp[\sigma t + im\theta]$ $\quad m \in \mathbb{Z}$

$\Rightarrow \sigma = 1 - m^2 \quad < 0$ for $|m| > 1$

Note $m = 0$ just corresponds to shift of time origin

$m = 1$, $\sigma = 0$ neutral, corresponds to translation of centre (shift in space origin)

(iii) $R = \bar{R} + \rho$,

again

$$c - \frac{1}{R} + \rho_t = c\left[1 + \frac{\rho_\theta^2}{(\bar{R}+\rho)^2}\right]^{1/2} - \frac{\left\{1 - \frac{\rho_{\theta\theta}}{\bar{R}+\rho} + 2\left(\frac{\rho_\theta}{\bar{R}+\rho}\right)^2\right\}}{(\bar{R}+\rho)\left[1 + \frac{\rho_\theta^2}{(\bar{R}+\rho)^2}\right]}$$

Assume $\bar{R} \gg 1$,

$$c - \frac{1}{R} + \rho_t = c\left[1 + \frac{1}{2}\frac{\rho_\theta^2}{\bar{R}^2}\cdots\right] - \frac{\left[1 - \frac{\rho_{\theta\theta}}{\bar{R}}\cdots + \frac{2\rho_\theta^2}{\bar{R}^2}\cdots\right]}{\bar{R}} \times$$

$$\left(1 - \frac{\rho}{\bar{R}}\cdots\right)\left(1 - \frac{\rho_\theta^2}{\bar{R}^2}\cdots\right)$$

So

$$c - \frac{1}{\bar{R}} + \rho_t = c + \frac{c\rho_\theta^2}{2\bar{R}^2} \cdots$$

$$- \frac{1}{\bar{R}}\left[1 - \frac{\rho_{\theta\theta}}{\bar{R}} + \frac{2\rho_\theta^2}{\bar{R}^2} \cdots\right]\left[1 - \frac{\rho}{\bar{R}} \cdots\right]\left[1 - \frac{\rho_\theta^2}{\bar{R}^2} \cdots\right]$$

$$\Rightarrow \rho_t = \frac{1}{\bar{R}} + \frac{c\rho_\theta^2}{2\bar{R}^2} \cdots - \frac{1}{\bar{R}}\left[1 - \frac{\rho_{\theta\theta}}{\bar{R}} - \frac{\rho}{\bar{R}} + O\left(\frac{1}{\bar{R}^2}\right)\right]$$

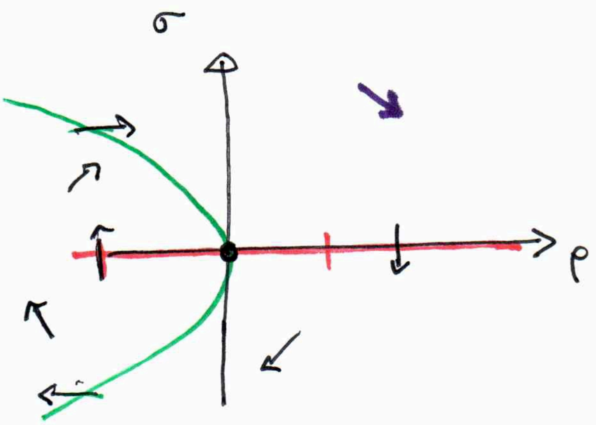
$$\rho_t = \frac{c\rho_\theta^2}{2\bar{R}^2} + \frac{(\rho_{\theta\theta} + \rho)}{\bar{R}^2} + \cdots$$

Define $\tau = \int_0^t \bar{R}^{-2}\, dt$

$$\Rightarrow \rho_\tau = \tfrac{1}{2}c\rho_\theta^2 + \rho_{\theta\theta} + \rho$$

Steady solutions $\quad \rho_{\theta\theta} + \tfrac{1}{2}c\rho_\theta^2 + \rho = 0$

$$\rho' = \sigma$$
$$\sigma' = -\left(\tfrac{1}{2}c\sigma^2 + \rho\right)$$




i $\rho$ nullcline

$\sigma$ nullcline

ii direction $(\sigma, \rho > 0)$

iii, rest of directions

iv fixed pt not saddle : node or spiral

v linearise $\begin{pmatrix}\rho\\ \sigma\end{pmatrix}' = \begin{pmatrix}0 & 1\\ -1 & 0\end{pmatrix}\begin{pmatrix}\rho\\ \sigma\end{pmatrix} \rightarrow$ centre!

is it actually a centre?

– is there a first integral (cf. Lotka–Volterra)

$$\frac{d\sigma}{d\rho} = -\frac{(\frac{1}{2}c\sigma^2 + \rho)}{\sigma}$$

ie $\frac{d}{d\rho}(\frac{1}{2}\sigma^2) = -\frac{1}{2}c\sigma^2 - \rho$

$$\frac{d}{d\rho}[\tfrac{1}{2}\sigma^2 e^{c\rho}] = -\rho e^{c\rho}$$

Note $\frac{d}{d\rho}[(A\rho+B)e^{c\rho}] = e^{c\rho}[cA\rho + cB + A] = -\rho e^{c\rho}$

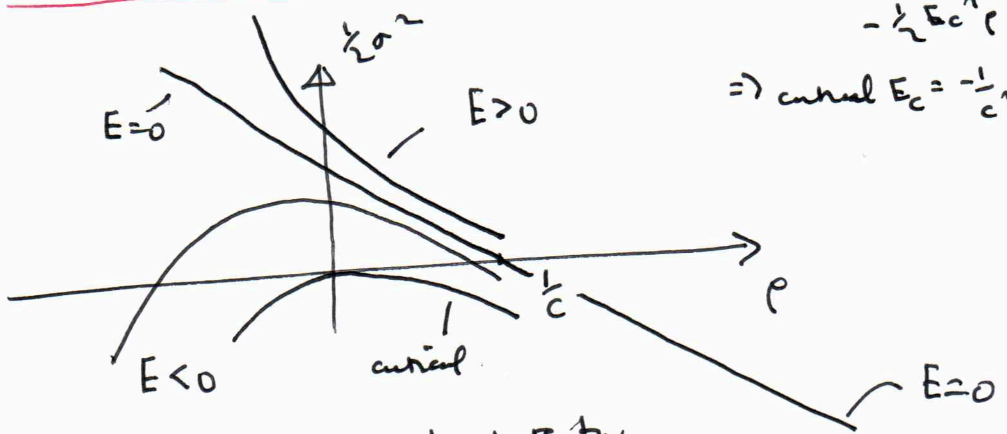
if $cA = -1$, $cB + A = 0 \Rightarrow A = -\frac{1}{c}$, $B = \frac{1}{c^2}$

$$\frac{d}{d\rho}[\tfrac{1}{2}\sigma^2 e^{c\rho}] - \frac{d}{d\rho}[(\tfrac{1}{c^2} - \tfrac{\rho}{c})e^{c\rho}] = 0$$

$\Rightarrow [\frac{1}{2}\sigma^2 + \frac{\rho}{c} - \frac{1}{c^2}]e^{c\rho} = E$ constant

and then $\frac{1}{2}\sigma^2 = Ee^{-c\rho} - \frac{\rho}{c} + \frac{1}{c^2}$

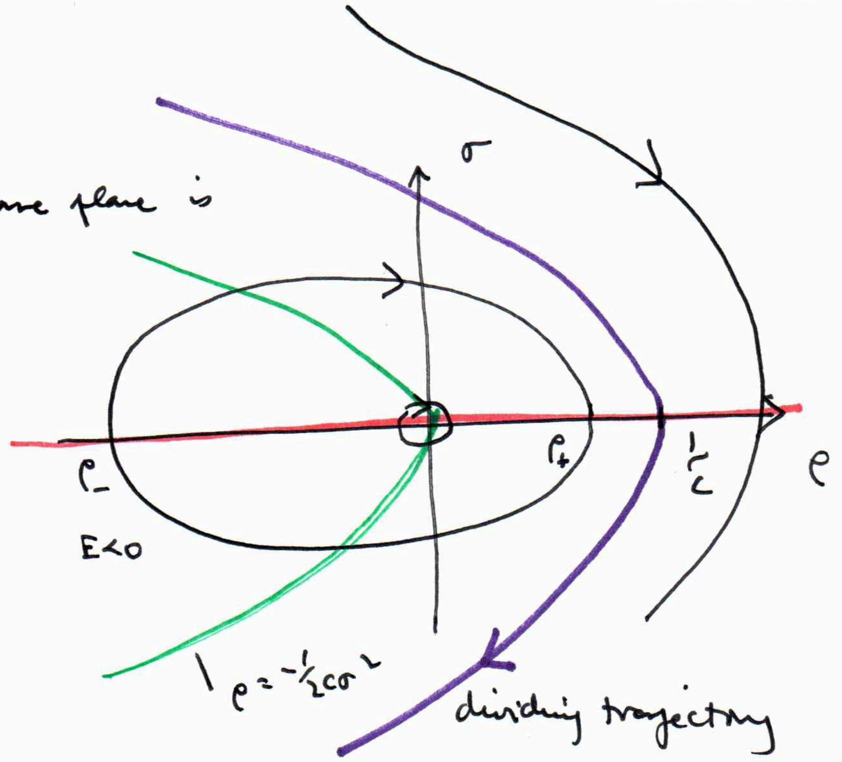
[note at $\rho \approx 0$,
$\frac{1}{2}\sigma^2 = E + \frac{1}{c^2} - c(E + \frac{1}{c^2})\rho$
$- \frac{1}{2}Ec^2\rho^2 \ldots$
$\Rightarrow$ critical $E_c = -\frac{1}{c^2}$ ]




so clearly we get closed orbits for $E<0$

unbounded for $E>0$ (small $-E$ gives large orbits
fixed pt is $E = -\frac{1}{c^2}$).

So phase plane is




Critical dividing trajectory on $E=0$ : $\frac{1}{2}\sigma^2 = \frac{1}{c^2} - \frac{\rho}{c}$ i.e. $\rho = \frac{1}{c} - \frac{1}{2}c\sigma^2$

So there are closed orbits for $\rho(\theta)$ where

$$-\frac{1}{c^2} < E < 0$$

but only those for which the period $P = \frac{2\pi}{m}$, $m \in \mathbb{N}$, have physical meaning. For $m=1$ they are target patterns: also for $m>1$ but 'crinkly'

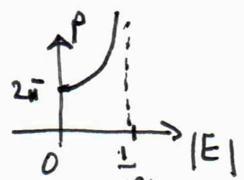
[Note: for $E<0$, the period is $P = 2\int_{\rho_{min}}^{\rho_{max}} \frac{d\rho}{\rho'} = \sqrt{2}\int_{\rho_{min}}^{\rho_{max}} \frac{d\rho}{[E e^{-c\rho} - \frac{\rho}{c} + \frac{1}{c^2}]^{1/2}}$

for $E<0$ $\quad P = \sqrt{2}\int_{\rho_{min}}^{\rho_{max}} \frac{d\rho}{\left[\frac{1}{c^2} - \frac{\rho}{c} - |E| e^{-c\rho}\right]^{1/2}}$

as $E \to 0$ $\quad P \to \infty$

as $E \to -\frac{1}{c^2}$, orbits near origin $\rho'' + \rho \simeq 0$ so $P = 2\pi$.

$P$ increases monotonically with $|E|$




So in fact $P > 2\pi$ for $E<0$

$\Rightarrow$ no target waves! ]

[Note: no spiral waves as no orbits with $\rho \to \infty$]

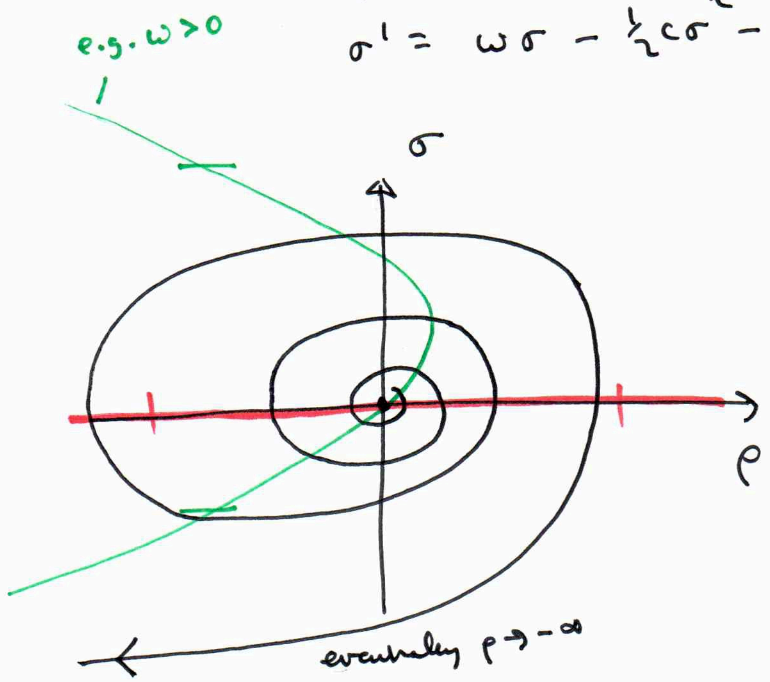
Now try $\rho = \rho(\eta)$, $\eta = \omega\tau - \theta$, $\omega \ll 1$

$$\rho_\tau = \tfrac{1}{2}c\rho_\theta^2 + \rho_{\theta\theta} + \rho$$

$$\Rightarrow \quad \omega\rho' = \tfrac{1}{2}c\rho'^2 + \rho'' + \rho$$

## Phase plane

$$\rho' = \sigma$$
$$\sigma' = \omega\sigma - \tfrac{1}{2}c\sigma^2 - \rho$$




i $\rho$ nullcline $\sigma = 0$

ii $\sigma$ $\rho = \omega\sigma - \tfrac{1}{2}c\sigma^2$
roots $\sigma = 0, \ \frac{2\omega}{c}$

iii trajectories as before

iv At $(0,0)$
with $\rho'' - \omega\rho' + \rho = 0$
unstable sp. if $\omega > 0$

With $E = \left(\tfrac{1}{2}\sigma^2 + \frac{\rho}{c} - \frac{1}{c^2}\right)e^{c\rho}$

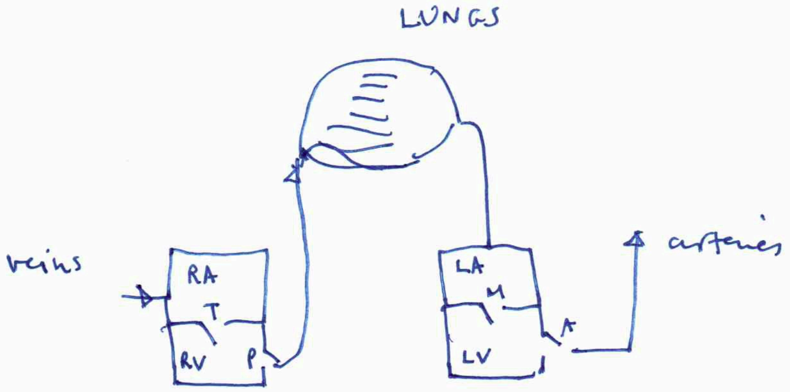
$$\Rightarrow E' = \left[\sigma\sigma' + \frac{\rho'}{c} + \left(\tfrac{1}{2}\sigma^2 + \frac{\rho}{c} - \frac{1}{c}\right)c\rho'\right]e^{c\rho}$$
$$= \left[\sigma\left(\omega\sigma - \tfrac{1}{2}c\sigma^2 - \rho\right) + \left(\tfrac{1}{2}\sigma^2 + \frac{\rho}{c}\right)c\sigma\right]e^{c\rho}$$
$$= \omega\sigma^2 e^{c\rho}.$$

The closed orbits with $\omega = 0$ have $E$ constant.

If $\omega > 0$ $E$ increases indefinitely

'spiral waves' possible to some extent... (but eventually $\rho \to -\infty$ $\therefore$)

4/




R, L right left

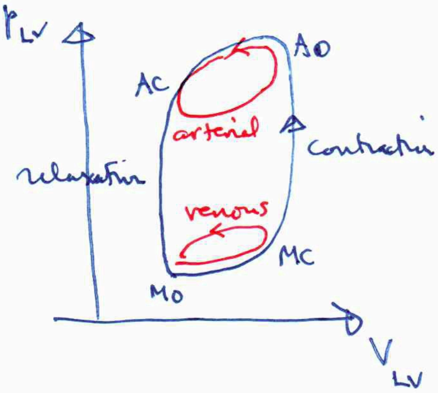
A, V atrium, ventricle

valves T tricuspid

P pulmonary

M mitral

A aortic




The pump action of the heart is effected by a contraction wave from the sino-atrial node which tightens the heart

Left-ventricular pressure $p_{LV}$ & volume $V_{LV}$ are related by

$$V_{LV} = V^0_{LV} + C_{LV} p_{LV}$$

At MC contraction causes $C_{LV}$ to drop.

Both valves are closed so $V_{LV}$ is constant and $p_{LV}$ increases (MC to AO)

At AO the aortic valve opens.

AO → AC ejection of blood occurs, $V_{LV}$ decreases until $p_{LV}$ reaches arterial pressure $p_a$, at AC the aortic valve closes.

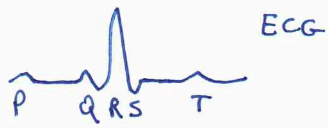
7

Also at AC the relaxation wave causes $c_{LV}$ to rise.

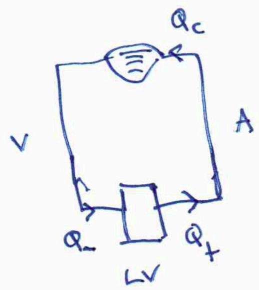
Both valves are closed, so $p_{LV}$ drops until it reaches the venous value, when the mitral valve opens, and filling occurs until the next contraction wave, $p_{LV} > p_v$ (venous) and the mitral valve closes at MC: then repeat.

SV Stroke volume : change in $V_{LV}$ between activation & relaxation

HR Heart rate : $\dfrac{1}{\text{RR interval}}$ for example




Blood flow rate = SV × HR




volumes $V_a$, $V_v$, $V_{LV}$ (arterial, venous, left ventricle)

$$\dot{V}_a = Q_+ - Q_c$$
$$\dot{V}_v = Q_c - Q_-$$
$$\dot{V}_{LV} = Q_- - Q_+$$

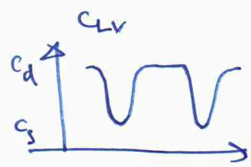
$Q_+$ $Q_-$ $Q_c$ blood flow to arteries, to capillaries, from veins

$$Q_c = \frac{p_a - p_v}{R_c} \qquad V_a = V_{a0} + C_a p_a$$

$$Q_+ = \frac{[p_{LV} - p_a]_+}{R_a} \qquad V_v = V_{v0} + C_v p_v$$

$$Q_- = \frac{[p_v - p_{LV}]_+}{R_v} \qquad V_{LV} = V_{LV0} + C_{LV} p_{LV}$$

&



# Math Physiol Problem set 3, q5 answer

5/

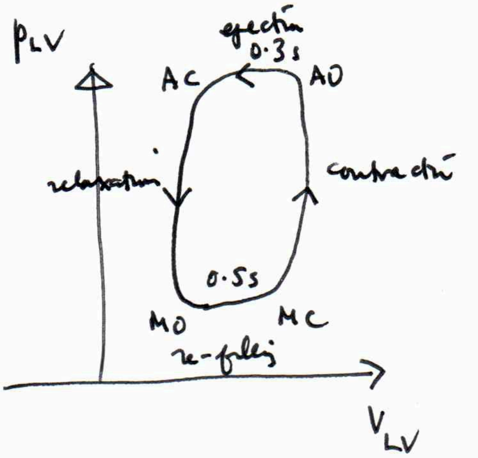
$$\dot{p}_a = \frac{-(p_a - p_v)}{R_c C_a} \; 1.8\,s + \frac{[p_{LV} - p_a]_+}{R_a C_a} \; 0.09\,s \qquad (1)$$

$$\dot{p}_v = \frac{p_a - p_v}{R_c C_v} \; 60\,s - \frac{[p_v - p_{LV}]_+}{R_v C_v} \; 0.7\,s \qquad (2)$$

$$\dot{V}_{LV} = \frac{[p_v - p_{LV}]_+}{R_v} - \frac{[p_{LV} - p_a]_+}{R_a} \;; \quad V_{LV} = V_0 + C_{LV} p_{LV} \qquad (3)$$

systole $$\dot{p}_{LV} = -\frac{(p_{LV} - p_a)}{R_a C_s} \; 0.02\,s \qquad (4)$$

diastole $$\dot{p}_{LV} = \frac{p_v - p_{LV}}{R_v C_d} \; 0.25\,s \qquad (5)$$




Start with $p_{LV}^0$, $p_v^0$, $p_a^0$ : & $C_{LV} = C_d$ so $C_{LV} p_{LV} = C_d p_{LV}^0$

1 Contraction is isovolumetric as both valves are closed $\Rightarrow \dot{V}_{LV} = 0$

$p_a$ & $p_v \simeq$ constant as short time scale compared to 1.8 s (a)
& 60 s (v)

3 Ejection.

Starts when $p_{LV} = p_a^0$ & thus $C_{LV} p_{LV} = C_{LV} p_a^0 = C_d p_{LV}^0$

(isovolumetric)

From (1) relaxation time for $p_a$ is 0·09 s

& $p_{LV}$ is 0·025 (from (4))

So $p_{LV} \simeq p_a$ after short transient

Add (1) & (3) ~~K(...)~~

$$\dot{(C_a p_a + C_{LV} p_{LV})} = \frac{-(p_a - p_v)}{R_c} \simeq \frac{-p_a}{R_c} \quad \text{as } p_v \ll p_a \quad (6)$$

over remainder of change of $C_{LV}$ (< 0·05 s, rapid)

$$C_a p_a + C_{LV} p_{LV} \simeq \text{constant} = C_a p_a^0 + C_d p_{LV}^0$$

& finishes with $C_{LV} = C_s$ and so

$$(C_a + C_s) p_a \simeq C_a p_a^0 + C_d p_{LV}^0$$

so $p_a$ jumps first from $p_a^0$ to $\dfrac{C_a p_a^0 + C_d p_{LV}^0}{C_a + C_s} = p^*$ (A)

Following this ~~...~~ (6) $\Rightarrow$ $(C_a + C_s)\dot{p}_a \simeq -\dfrac{p_a}{R_c}$

so $p_a \simeq p^* e^{-\lambda_1 t}$ $\qquad \lambda_1 = \dfrac{1}{R_c(C_a + C_s)}$

Additionally (mitral valve closed) $\dot{p}_v \simeq \dfrac{p_a}{R_c C_v}$ so $p_v \simeq p_v^0 + \dfrac{p^*}{\lambda_1 R_c C_v}\left[1 - e^{-\lambda_1 t}\right]$

So at end ejection $(t = \Delta t_F)$ [(when $C_{LV}$ starts to rise & aortic valve closes)

$$p_a = p_a^1 = \Delta_1 p^* \qquad \Delta_1 = e^{-\lambda_1 \Delta t_F} \qquad \text{B}$$

$$p_v = p_v^1 = p_v^0 + \frac{(C_a + C_s) p^*}{C_v}(1 - \Delta_1) \qquad \text{C}$$

3. Relaxation

$p_a, p_v$ constant as dv is no shunt

$C_{LV} p_{LV}$ starts at $C_s p_a^1$

and when $p_{LV} = p_v^1$ the mitral valve opens

so $C_{LV} p_{LV} = C_s p_a^1 = C_{LV} p_v^1$ at that point

ie $C_{LV} = \frac{C_s p_a^1}{p_v^1}$ : ($< C_d$ : so $C_{LV}$ continues to $C_d$ after mitral valve opens. However the time constants in (1) & (5) (1.8s & 0.25s) are not small enough for $p_v$ or $p_a$ to change so $C_{LV}$ carries on up to $C_d$ .)

So at end $C_{LV} p_{LV} = C_s p_a^1 = C_d p_{LV}^1$

ie $p_{LV}^1 = \frac{C_s p_a^1}{C_d}$ (6) D

4. Refilling

Approximately $\dot{p}_{LV} = \frac{p_v - p_{LV}}{R_v C_d}$

$$\dot{p}_a \approx -\frac{p_a}{R_c C_a} \implies p_a = p_a^1 e^{-\lambda_2 t}, \ \lambda_2 = \frac{1}{R_c C_a}$$

$$\dot{p}_v \approx \frac{p_a}{R_c C_v} - \frac{(p_v - p_{LV})}{R_v C_v}$$

and then (volume conservation)

$$\dot{\left( C_a p_a + C_v p_v + C_d p_{LV} \right)} = 0 \qquad \text{(add (1),(2),(5))}$$

$$\Rightarrow C_a p_a + C_v p_v + C_d p_{LV} = C_a p_a^1 + C_v p_v^1 + \underbrace{C_d p_{LV}^1}_{= C_s p_a^1 \text{ from (6) on p3}}$$

$$= (C_a + C_s) p_a^1 + C_v p_v^1$$

subtracting $p_{LV}$ eq from $p_v$ eq in refilling

$$\dot{(p_v - p_{LV})} = \frac{p_a}{R_c C_v} - \underbrace{\left[ \frac{1}{R_v C_v} + \frac{1}{R_v C_d} \right]}_{\lambda_3 = \frac{1}{R_v}\left(\frac{1}{C_v} + \frac{1}{C_d}\right)} (p_v - p_{LV})$$

$$\text{so } \dot{\left[ (p_v - p_{LV}) e^{\lambda_3 t} \right]} = \frac{p_a^1}{R_c C_v} e^{-\lambda_2 t} e^{\lambda_3 t}$$

note $\lambda_3 - \lambda_2 = \frac{1}{R_v}\left(\frac{1}{C_v} + \frac{1}{C_d}\right) - \frac{1}{R_c C_a} = \frac{1}{\mu R_c C_v}$

$$\text{using } \mu = \frac{1}{R_c C_v \left[ \frac{1}{R_v}\left(\frac{1}{C_v} + \frac{1}{C_d}\right) - \frac{1}{R_c C_a} \right]}$$

$$\text{so } (p_v - p_{LV}) e^{\lambda_3 t} = \frac{p_a^1}{(\lambda_3 - \lambda_2) R_c C_v} \left[ e^{-\lambda_2 t + \lambda_3 t} - 1 \right] + (p_v^1 - p_{LV}^1)$$

to satisfy $p_v = p_v^1$, $p_{LV} = p_{LV}^1$ at $t = 0$

Using the definition of $\mu$ this produces

$$p_v - p_{LV} = \mu p_a^1 \left[ e^{-\lambda_2 t} - e^{-\lambda_3 t} \right] + (p_v^1 - p_{LV}^1) e^{-\lambda_3 t}$$

until $t = \Delta t_R$ where we thus have (with superscript $\S$ 2)

$$p_a^2 = \Delta_2 p_a^1 \quad \text{(E)} \qquad \Delta_2 = e^{-\lambda_2 \Delta t_R}$$

define $\Delta = p_v^2 - p_{LV}^2$ ; from above

$$\Delta = \mu p_a^1 (\Delta_2 - \Delta_3) + (p_v^1 - p_{LV}^1) \Delta_3 \quad \text{(F)} \qquad \Delta_3 = e^{-\lambda_3 \Delta t_R}$$

then from

$$C_a p_a + C_v p_v + C_d p_{LV}$$
$$= C_a p_a + (C_v + C_d) p_v - C_d (p_v - p_{LV}) = (C_a + C_s) p_a^1 + C_v p_v^1$$

we have

$$p_v^2 = \frac{1}{(C_v + C_d)} \left[ (C_a + C_s) p_a^1 + C_v p_v^1 + C_d \Delta - C_a p_a^2 \right] \quad \text{(G)}$$

& then $p_{LV}^2 = p_v^2 - \Delta$ (H)

Working our way through them, from
$p_a^0, p_v^0, p_{LV}^0$ via $p^*$ (A) $p_a^1$ (B) $p_v^1$ (C) $p_{LV}^1$ (D) and $\Delta$ (F)

to $p_a^2$ (E), $p_v^2$ (G) & $p_{LV}^2$ (H)

each map is linear and homogeneous thus $\begin{pmatrix} p_a^2 \\ p_v^2 \\ p_{LV}^2 \end{pmatrix} = A \begin{pmatrix} p_a^0 \\ p_v^0 \\ p_{LV}^0 \end{pmatrix}$

but is subject to end diastolic constraint
$C_a p_a + C_v p_v + C_d p_{LV} = \text{constant} \Rightarrow$ unique steady state □