Problem sheet 3

1.1.

1). See lecture notes for derivation of the cable equation.

The resting potential V_{eq} is the potential at which $I_1(V) = 0$.

Using the non-dimensionalization given and substituting this into the cable equation and the gate variable equation gives the required stated equations where

$$\varepsilon = \sqrt{\frac{d}{4l^2 g_{Na} R_c}} \quad \text{and} \quad \varepsilon = \frac{C_m}{g_{Na} T_n}$$

so, setting these equal to one another gives

$$l = \frac{T_n}{2C_m}\left(\frac{g_{Na} d}{R_c}\right)^{\frac{1}{2}}.$$

Using the values given gives $\varepsilon \simeq 1.6 \times 10^{-3}$

$l \simeq 32.7$ cm.

This is of concern because this value is much longer than the axon itself, so the model is inappropriate as the lengthscale over which we anticipate excitations exceeds the length of the axon.

2).
$$\dot{u} = \mu - u - \gamma \dot{v}$$
$$\varepsilon \dot{v} = f(u,v)$$

$$f(u,v) = \beta\left(\frac{u^n}{1+u^n}\right) - \left(\frac{v^m}{1+v^m}\right)\left(\frac{u^p}{\alpha^p+u^p}\right) - \delta v$$

v-nullcline is $f(u,v) = 0$.

If $\delta \ll 1$ this gives $\frac{v^m}{1+v^m} = \beta\left(\frac{\frac{u^n}{1+u^n}}{\frac{u^p}{\alpha^p+u^p}}\right)$ $n=2$, $p=4$

to leading order in δ.

Let $F = \frac{\beta u^n}{1+u^n}$, $G = \frac{u^p}{\alpha^p+u^p}$. Then $v = \left(\frac{\frac{F}{G}}{\frac{F}{G}-1}\right)^{1/m}$

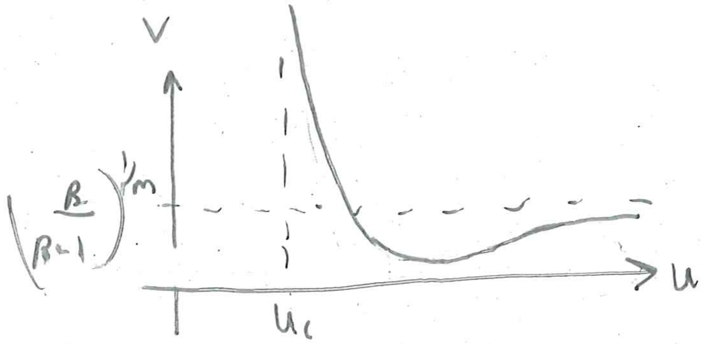
As $\frac{F}{G} \to 1$, $v \to \infty$. When $\frac{F}{G} \to 1$, $u \to u_c$, say

As $u \to \infty$, $F \to \beta$, $G \to 1$, so $v \to \left(\frac{\beta}{\beta-1}\right)^{1/m}$

For $u \gg 1$, $F \sim \beta\left(1 - \frac{1}{u^n}\right)$, $G \sim 1 - \left(\frac{u}{\alpha}\right)^p$

$\frac{F}{G} \sim \beta\left(1 - \frac{1}{u^n}\right)$ (since $n < m$) so v is increasing as $u \to \infty$

Overall, this gives a sketch:



Our neglection of the term δv when $\delta \ll 1$ breaks down as $v \to \infty$, specifically when $v = O(\frac{1}{\delta})$. Rescale

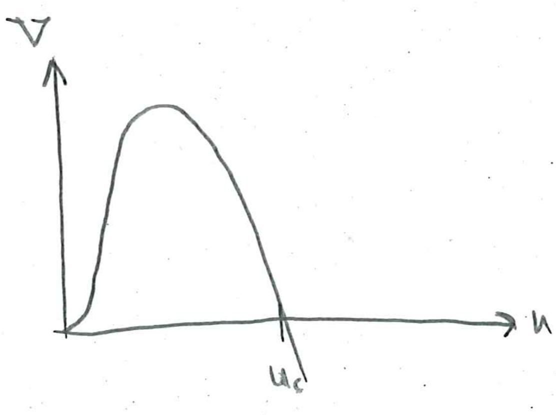
$v = \frac{V}{\delta}$ to find

$$\beta \frac{u^n}{1+u^n} - \left(1 + \frac{\delta^n}{V^m}\right)^{-1}\left(\frac{u^p}{\alpha^p + u^p}\right) - V = 0.$$

Now taking the limit $\delta \ll 1$ gives

$$V = \beta \frac{u^n}{1+u^n} - \frac{u^p}{\alpha^p + u^p}$$

As $u \to 0$, $V \to 0$



Now consider intermediate regime.

Rescale $u = u_c + \upsilon U$

$v = \lambda W$ $\qquad \upsilon \ll 1,$

$\lambda \gg 1.$

$$f(u,v) = 0 \Rightarrow F(u) - G(u)\left(\frac{v^m}{1+v^m}\right) - \delta v = 0$$

$$\Rightarrow F(u_c) + \upsilon U F'(u_c) - \left(G(u_c) + \upsilon U G'(u_c)\right) \times \left(\frac{1}{1+\frac{1}{(\lambda W)^m}}\right) - \delta\lambda W = 0$$

$$\upsilon U\left(F'(u_c) - G'(u_c)\right) - G(u_c)\cdot\frac{1}{\lambda^m W^m} - \delta\lambda W + \ldots = 0$$

since $F(u_c) = G(u_c)$

by definition of u_c.

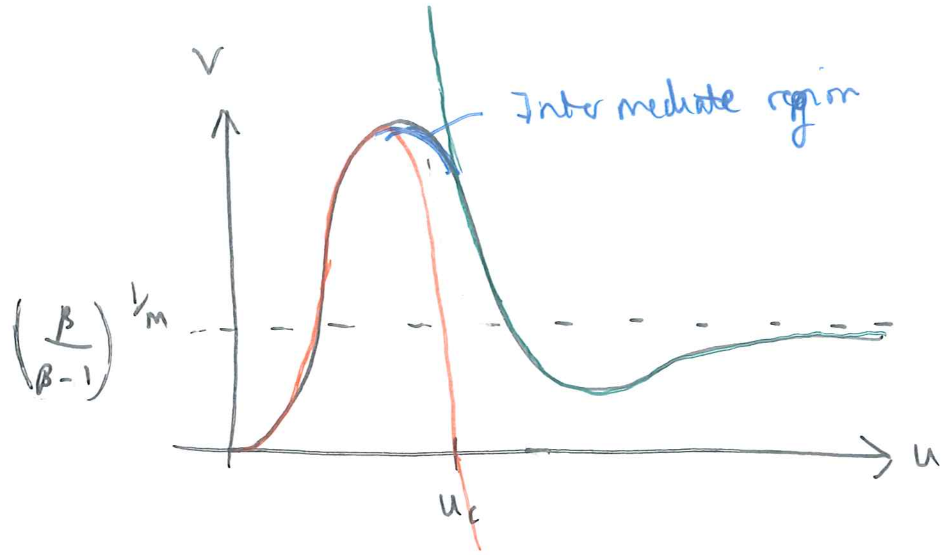
For a balance we require $\upsilon = \frac{1}{\lambda^m} = \delta\lambda$

$\Rightarrow \lambda^{m+1} = \frac{1}{\delta} \Rightarrow \lambda = \frac{1}{\delta^{1/m+1}}$

$\upsilon = \frac{1}{\lambda^m} = \delta^{\frac{m}{m+1}}$

as required

Putting these two results together gives an overall approximation for v:

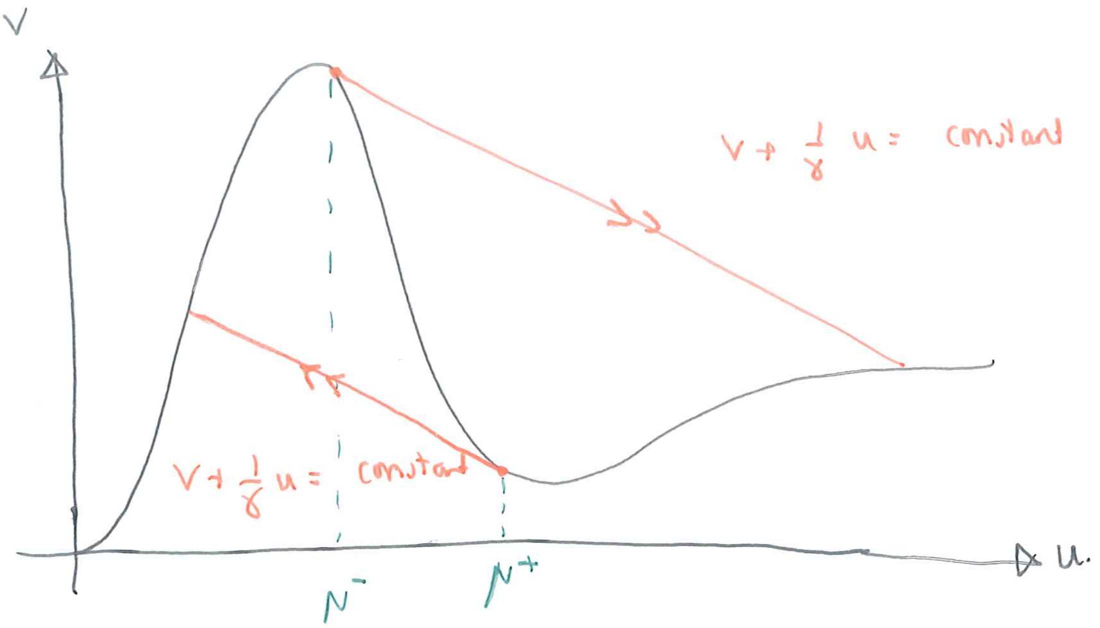


Now we have our v-nullcline we can draw the phase plane. When the system is not on the slow phase v-nullcline we have a fast phase. Rescaling $t = \varepsilon T$ gives

$$\frac{1}{\varepsilon}\frac{du}{dT} = \mu - u - \frac{\gamma}{\varepsilon}\frac{dv}{dT} \quad ①$$

$$\frac{dv}{dT} = f(u, v) \quad ②$$

① $\Rightarrow$ $u + \gamma v =$ constant on the fast phase.



$\mu^\pm$ are the places on the curve $f(u,v) = 0$ where the gradient is $-\frac{1}{\gamma}$

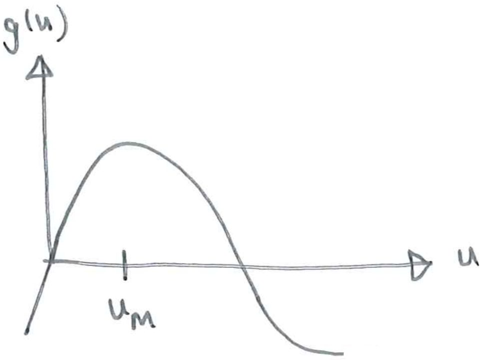
If $\mu_- < \mu < \mu_+$ then $\frac{d}{dt}(u + \gamma v) = \mu - u < 0$ when $u > \mu^+$

> 0 when $u < \mu^-$

This leads to self sustained or relaxation oscillations.

3)
$$u_t + \gamma v_t = \mu - u + \varepsilon u_{xx}$$
$$\varepsilon v_t = g(u) - v.$$

$\varepsilon \ll 1$, $\mu, \gamma \sim 1$



This is a specific case of the set-up considered in lectures.

Seek travelling wave solutions:

$$u = u(\xi), \quad v = v(\xi), \quad \xi = x + st, \quad s > 0.$$

$$\Rightarrow \quad s(u' + \gamma v') = \mu - u + \varepsilon u''$$
$$\varepsilon s v' = g(u) - v.$$

$\varepsilon \ll 1$ means that to leading order, $v = g(u)$ so the solution jumps quickly onto this curve.

We rescale $\xi = \varepsilon X$ to determine how we jump onto this curve.

This gives

$$s(u' + \gamma v') = u'' \quad ①$$

$$\boxed{sv' = g(u) - v} \quad ②$$

to leading order in ε, where $' = \frac{d}{dx}$

These two equations

Integrate ① to get

$$u' = s(u + \gamma v) + \text{constant} \quad (*)$$

$$\text{so} \quad v = -\frac{1}{\gamma} u + \underbrace{\frac{u' - \text{constant}}{\gamma s}}$$

this is a number that changes with x, which parameterises the curve.

These two equations form a pair of first order equations for the fast phase

As $x \to \pm \infty$ we will move to the start and end points of the fast phase, where we have $v = g(u)$. Here we are in quasi-static equilibrium, so as $x \to \pm\infty$, $u' = \frac{du}{dx} \to 0$. And so constant in $(*) = 0$ so $\boxed{u' = s(u + \gamma v)}$

In $(*)$ this gives

$$[u']_{-\infty}^{\infty} = [s(u + \gamma v)]_{-\infty}^{\infty}$$

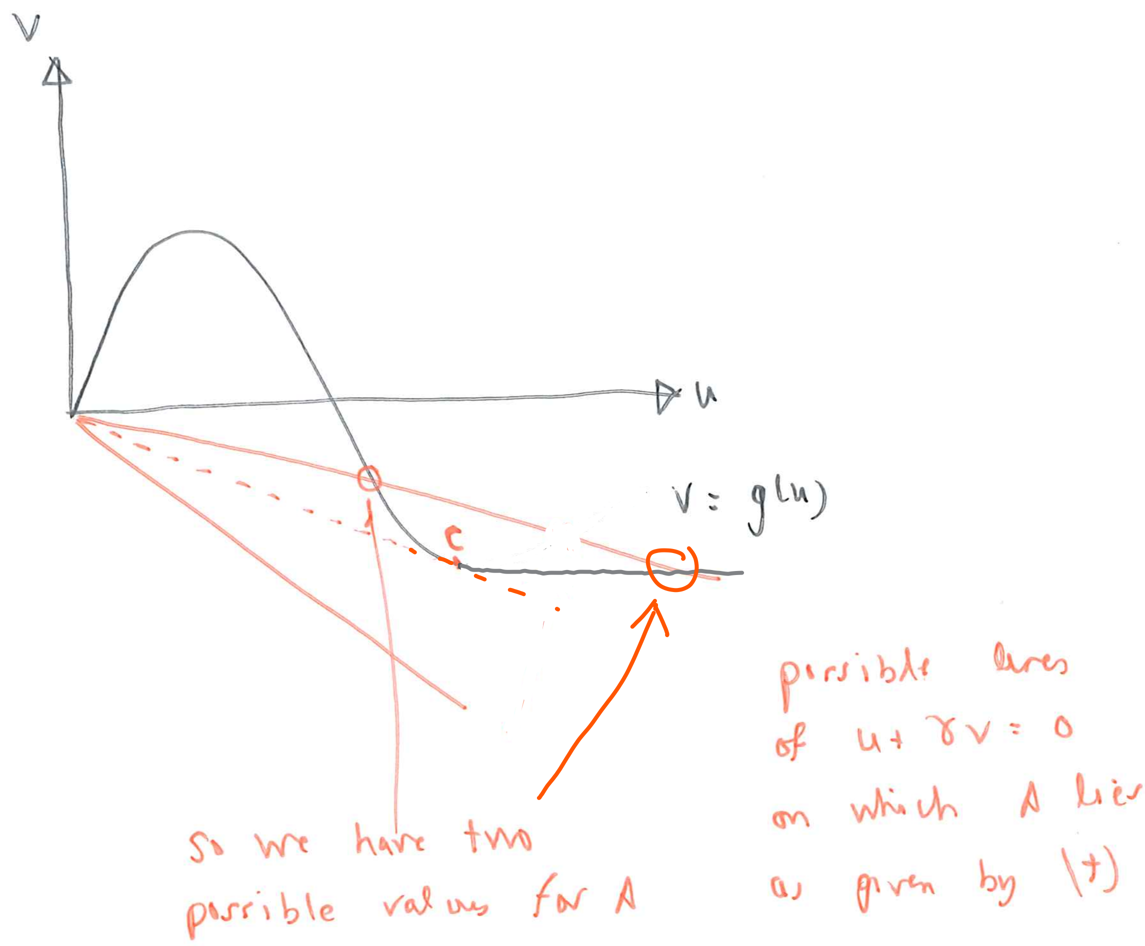
$$0 = [s(u + \gamma v)]_{-\infty}^{\infty}$$

Now $u = v = 0$ at the origin so the fast phase curve that takes us from the origin to a point A has $u + \gamma v = 0$ at point A.

So at A, $u + \gamma v = 0$ and $v = g(u)$ (†)

so $\boxed{u + \gamma g(u) = 0 \quad \text{at } A.}$

For a given value of γ we could either have no solutions for A or two solutions:



To have two possible values for A we need the line $u + \gamma v = 0$ to be above the dotted line,

This line has gradient $\frac{1}{\gamma_c}$ where at the point C we have the same gradient on the curve $v = g(u)$

So we have $\frac{1}{\gamma_c} = g'(u)$ at c

gradient of $v = g(u)$

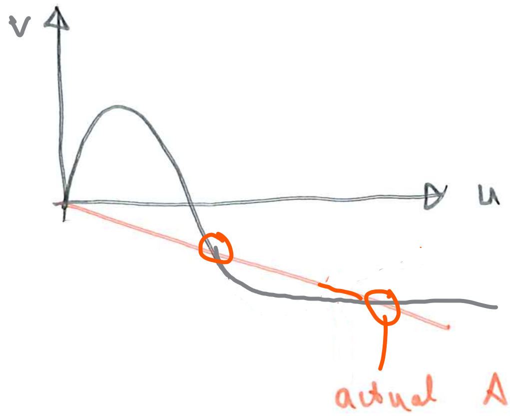
Thus we need $\boxed{\gamma > \gamma_c = \frac{1}{g'(u)}}$

And at c we have $u + \gamma v = 0$ and $v = g(u)$

so $u + \gamma g(u) = 0$

$$\boxed{u + \frac{g(u)}{g'(u)} = 0}$$ since $\gamma = \frac{1}{g'(u)}$

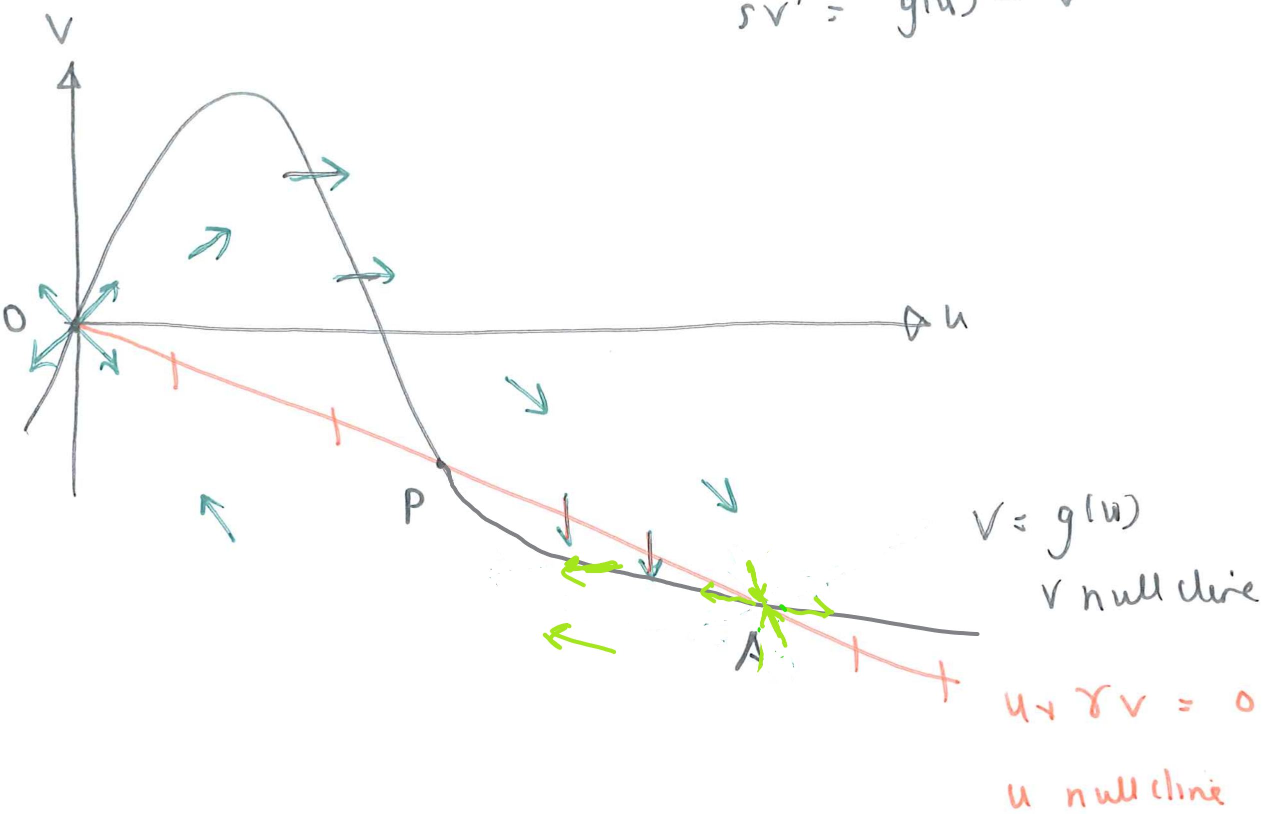
The actual A point is the one for which u_A takes the largest value as this corresponds to a saddle. (O and A join up the separatrices.) The other fixed point is a spiral (see below).



Phase plane

$$u' = s(u + \gamma v)$$

$$s v' = g(u) - v$$



O and A are saddles

P is a spiral

Stability of P : set $u = u_p + \mathcal{U}$, $v = v_p + \mathcal{V}$.

Linear stability analysis gives $\begin{pmatrix} \mathcal{U} \\ \mathcal{V} \end{pmatrix}' = \begin{pmatrix} s & \gamma s \\ \frac{g'}{s} & -\frac{1}{s} \end{pmatrix} \begin{pmatrix} \mathcal{U} \\ \mathcal{V} \end{pmatrix}$

$\text{trace}(\underline{\underline{M}}) = s - \frac{1}{s} < 0$ if $s < 1$

> 0 if $s > 1$

so stable if $s < 1$.

4)
$$u' = s(u + \gamma v) \quad ①$$
$$s v' = g(u) - v. \quad ②$$

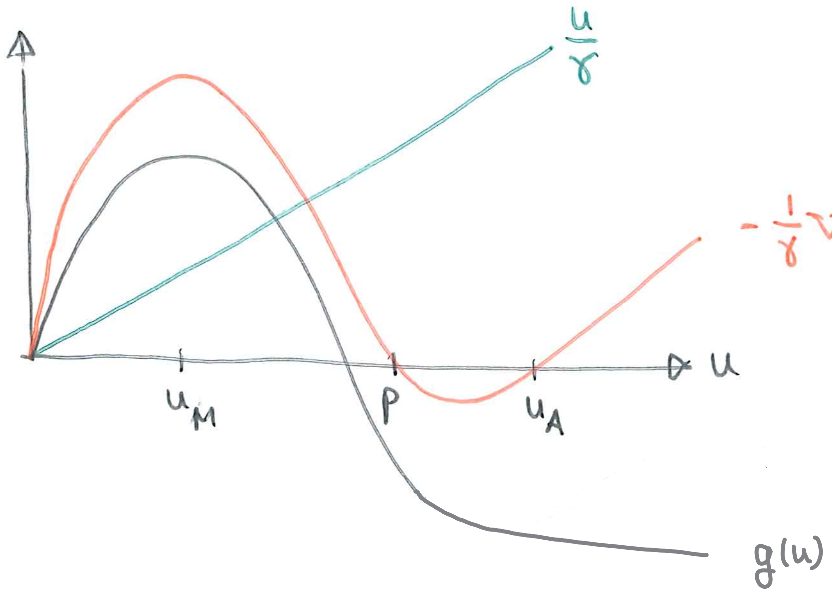
① $\Rightarrow$ $v = \frac{1}{\gamma s}(u' - us)$

In ② this gives $\frac{1}{\gamma}(u'' - su') = g(u) - \frac{1}{\gamma s}(u' - us)$

$$\Rightarrow \boxed{u'' - \left(s - \tfrac{1}{s}\right)u' + V'(u) = 0 \quad \text{where } V' = -\gamma g(u) - u}$$

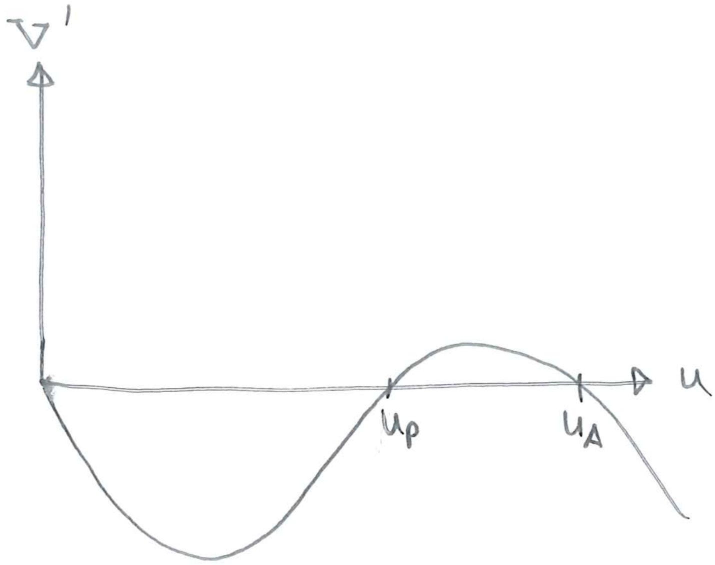
as required.

$\Rightarrow$ $V = -\frac{1}{2}u^2 - \gamma \int_0^u g(u)\, du$ if $V(0) = 0$.

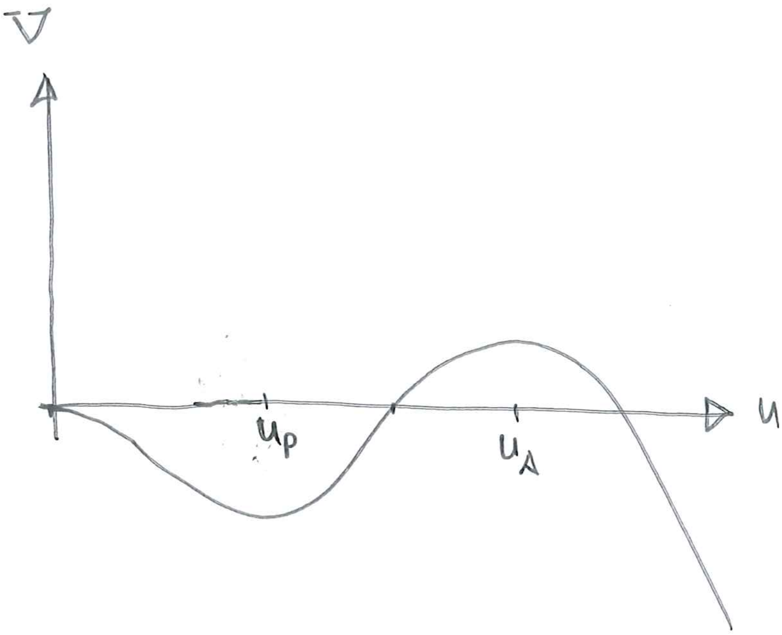


(we assume there are three roots)

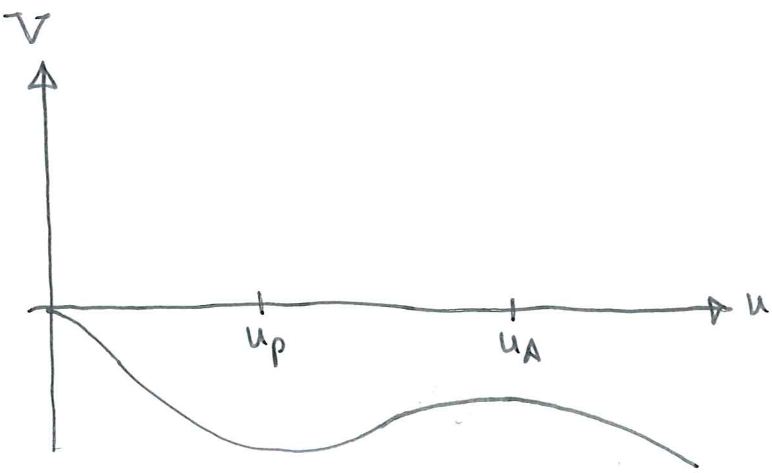
So



So



if $V(u_A) > 0$



if $V(u_A) < 0$.

Consider $E \stackrel{\text{def}}{=} \frac{1}{2}(u')^2 + V(u)$

So
$$\frac{dE}{dx} = u'\left(u'' + V'(u)\right)$$
$$= \left(s - \frac{1}{s}\right)(u')^2$$

At 0 and A, $u' = 0$

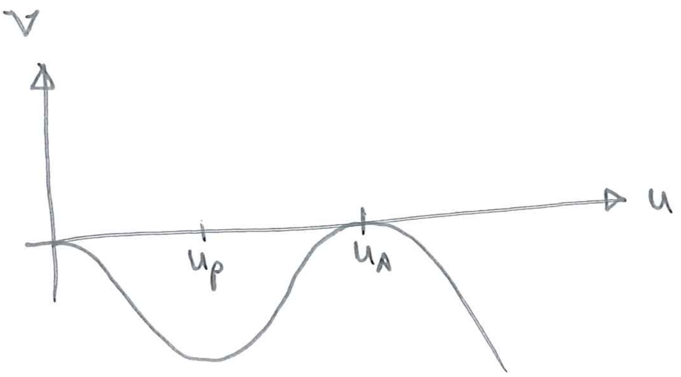
So at 0 and A, $E = V$.

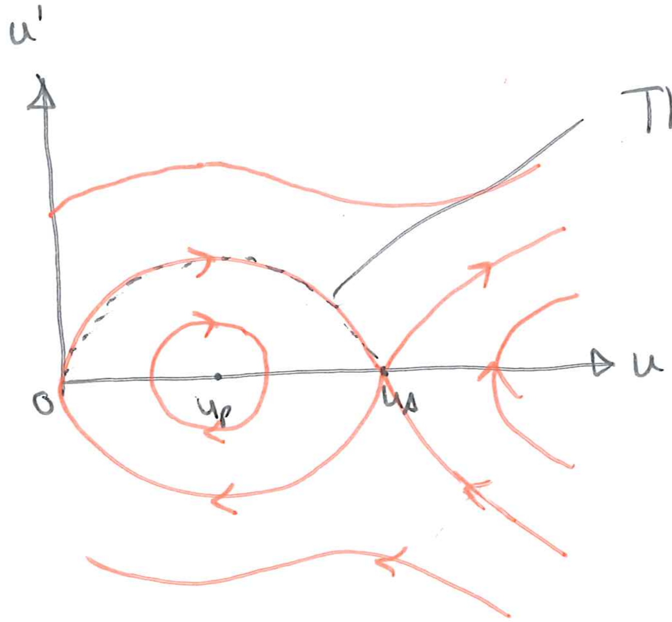
Thus, if $s > 1$ then $\frac{dE}{dx} > 0$ so we would need $V > 0$

and if $s < 1$ then $\frac{dE}{dx} < 0$ so we would need $V < 0$.

If $s = 1$ then $\frac{dE}{dx} = 0$ so energy is conserved and we have a conservative oscillator. (The equations are the same as for a simple pendulum but with a different potential.)

Thus the phase plane looks like thus :





There is a unique trajectory from 0 to A.

0 and A are saddles and P is a centre.