

Mathematical Cell Biology Graduate Summer Course
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Traveling Waves in a bistable Reaction-Diffusion System



www.math.ubc.ca/~keshet/MCB2012/

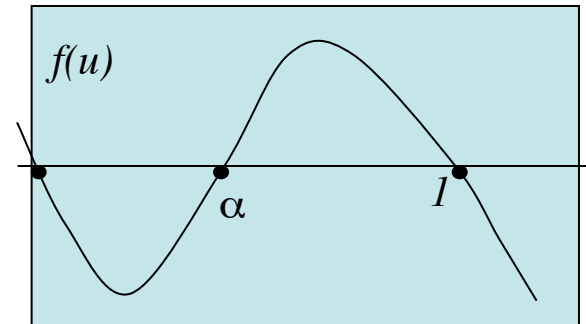
Wave phenomena in RD systems

Keener & Sneyd (1998) Mathematical Physiology; p 270-275

$$\frac{\partial u}{\partial t} = f(u) + D \frac{\partial^2 u}{\partial x^2}, \quad \frac{\partial u}{\partial x} \Big|_{\pm\infty} = 0$$

With f cubic: $f(u) = au(u-1)(\alpha-u)$ $0 < \alpha < 1$

...



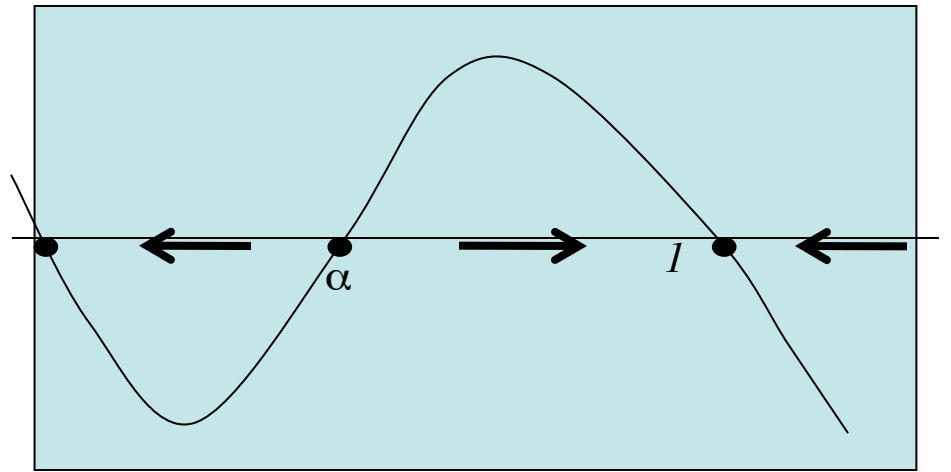
U is the shape of the wave, z is the position along the wave front

Bistable well-mixed system

$$\frac{\partial u}{\partial t} = f(u)$$

Steady states:

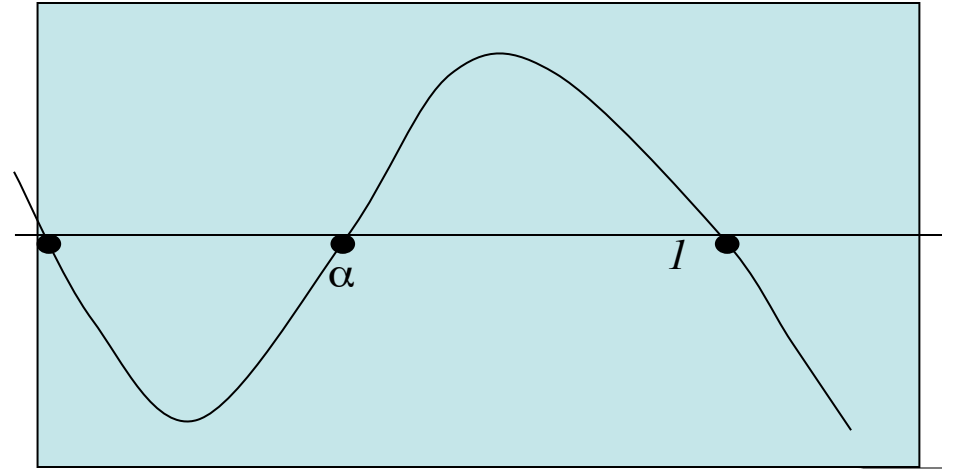
$$u = 0, \alpha, 1$$



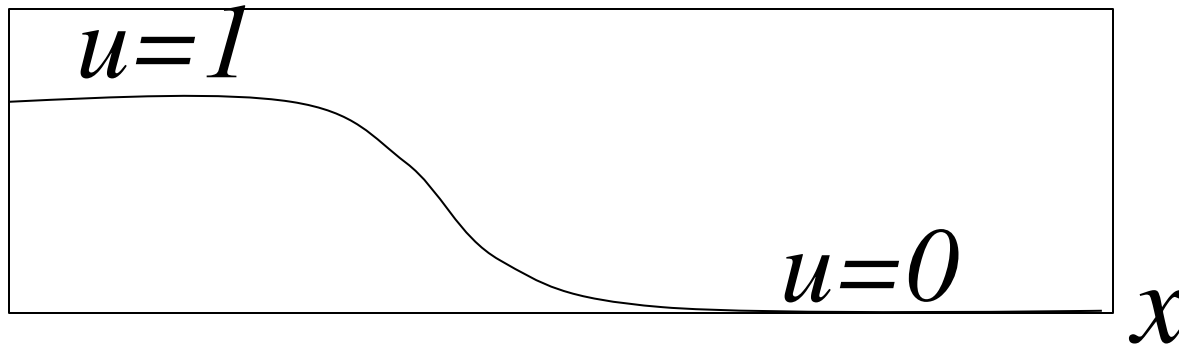
$$f(u) = au(u-1)(\alpha-u) \quad 0 < \alpha < 1$$

With diffusion

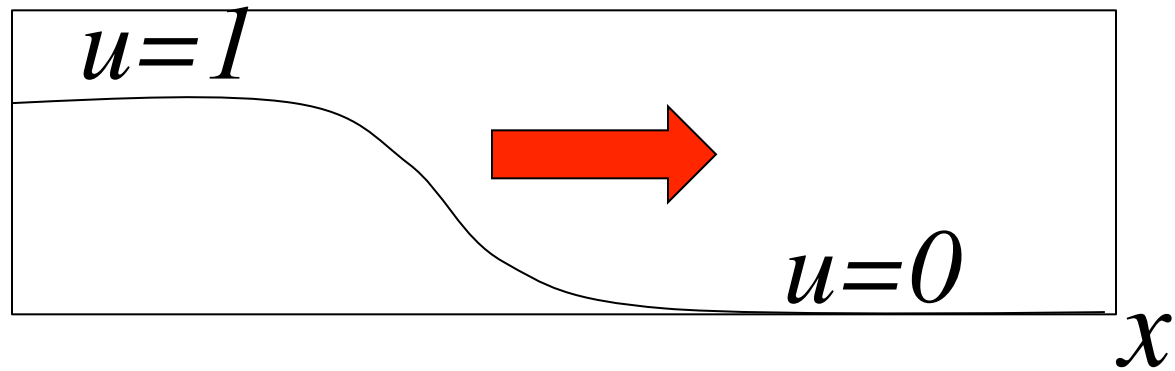
$$\frac{\partial u}{\partial t} = f(u) + D \frac{\partial^2 u}{\partial x^2}$$



$$f(u) = au(u-1)(\alpha-u) \quad 0 < \alpha < 1$$

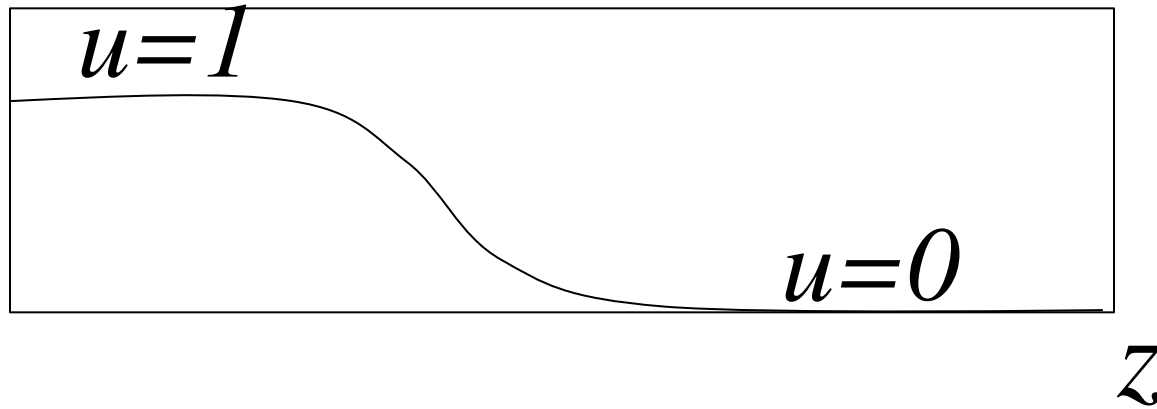


Moving Wave



Wave profile

Traveling wave coordinates: $z=x-ct$, $U(z)=u(x,t)$



What is the wave profile?

Traveling wave coordinates: $z=x-ct$, $U(z)=u(x,t)$

Scaling and transformation of coordinates:

$$\begin{array}{ccc} \frac{\partial}{\partial t} \rightarrow -c \frac{d}{dz} & \frac{\partial}{\partial x} \rightarrow \frac{d}{dz} & \\ \text{PDE} & \boxed{\frac{\partial u}{\partial t} = f(u) + \frac{\partial^2 u}{\partial x^2}} \rightarrow \boxed{-c \frac{dU}{dz} = f(U) + \frac{d^2 U}{dz^2}} & \text{ODE} \end{array}$$

2nd order (nonlin) ODE $U_{zz} - cU_z + f(U) = 0$

Equivalent ODE system:
$$\begin{cases} U_z = W \\ W_z = cW - f(U) \end{cases}$$

We can study this qualitatively in the UW phase plane to get insight into the shape of the wave.

$$\frac{\partial u}{\partial t} = f(u) + \frac{\partial^2 u}{\partial x^2}$$

(Rescaled)

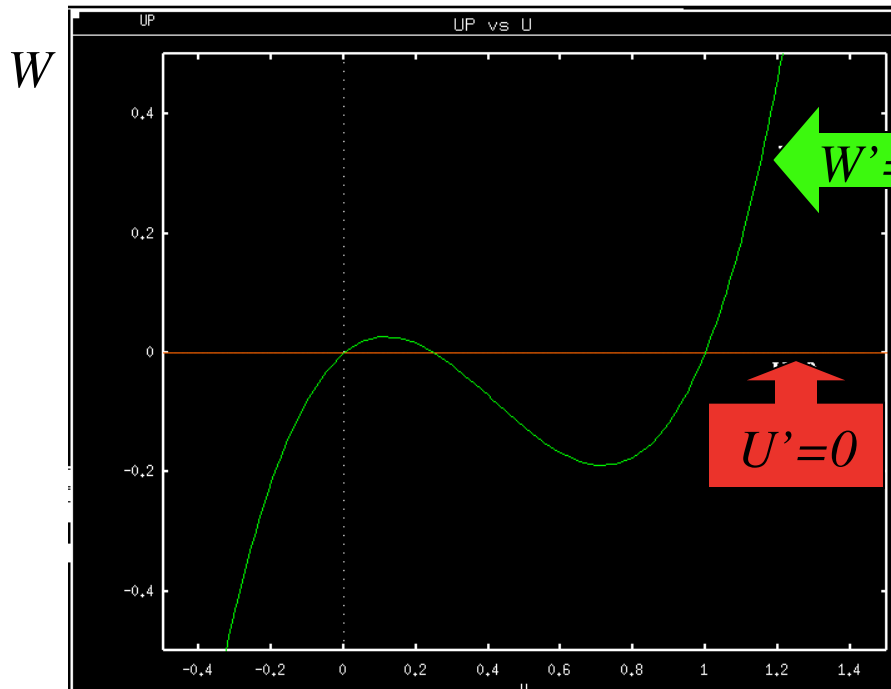
Example:

$$f(u) = u(1-u)(u-\alpha)$$

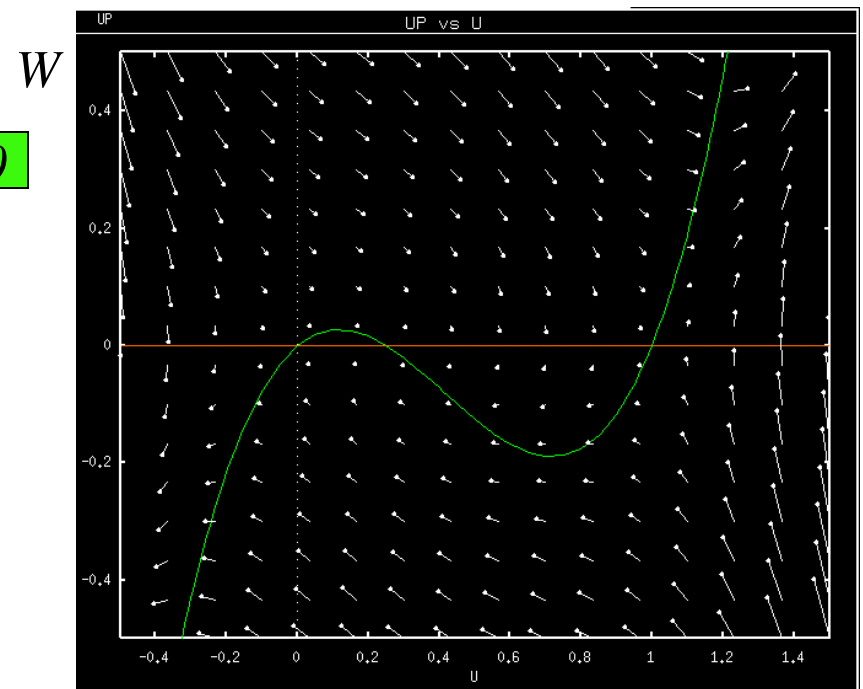
$$U_{zz} - cU_z + f(U) = 0$$

$$U_z = W$$

$$W_z = cW - f(U)$$



U



U

Bard Ermentrout's XPP file

Bistable.ode

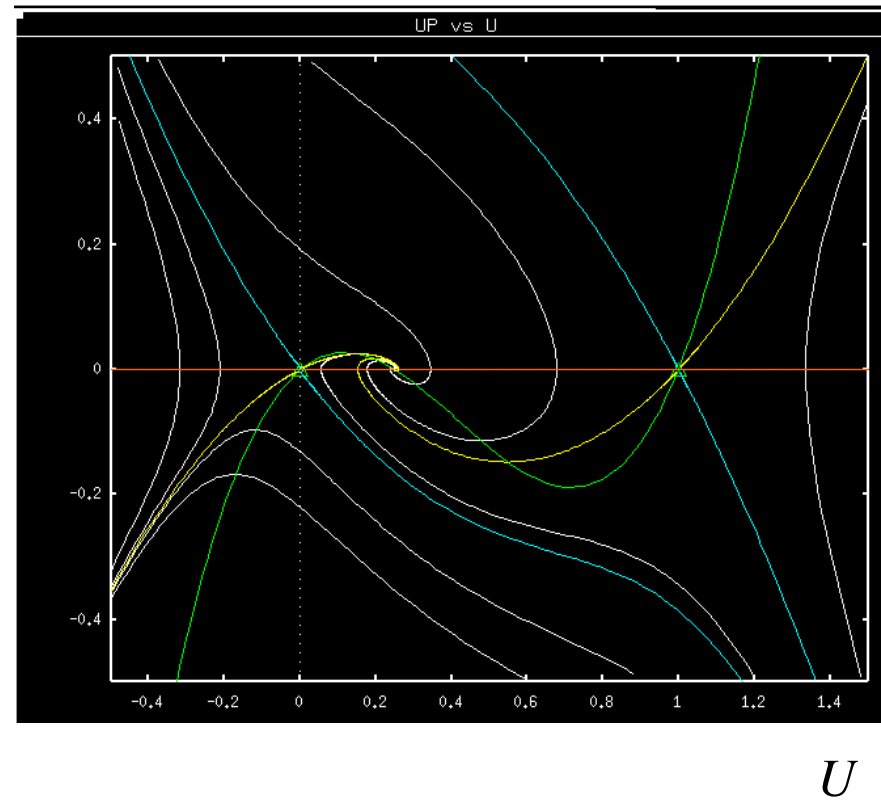
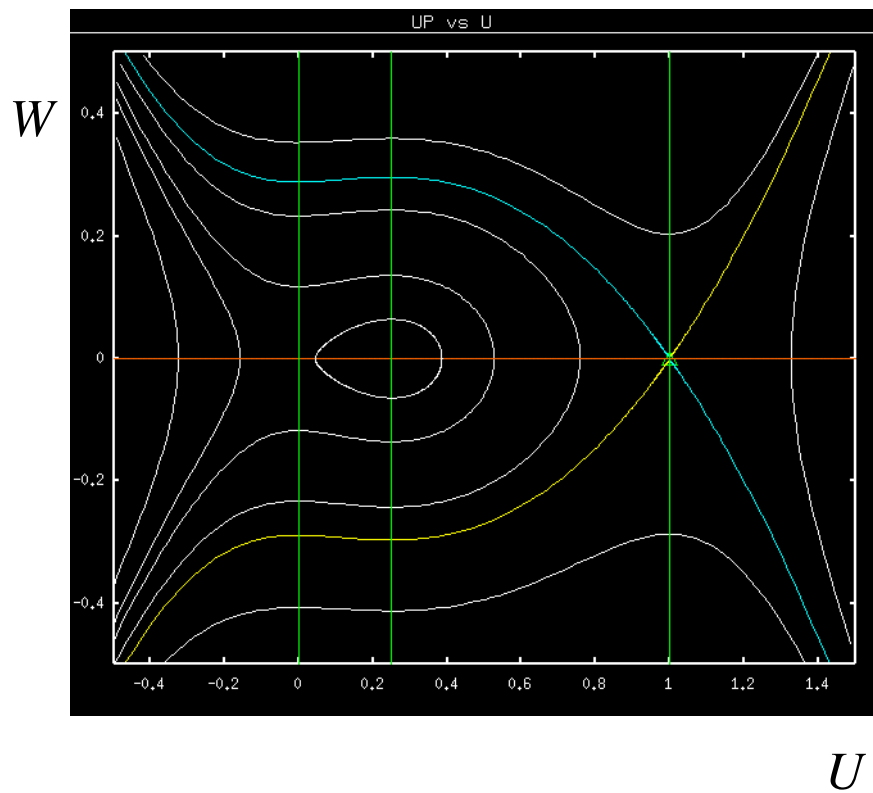
Xpp file

```
# bistable.ode
# classic example of a wave joining 0 and 1
#  $u_t = u_{xx} + u(1-u)(u-a)$ 
#
#  $-cu' = u'' + u(1-u)(u-a)$ 
f(u)=u*(1-u)*(u-a)
par c=0,a=.25
u'=up
up'=-c*up-f(u)
init u=1
@ xp=u,yp=up,xlo=-.5,xhi=1.5,ylo=-.5,yhi=.5
done
```

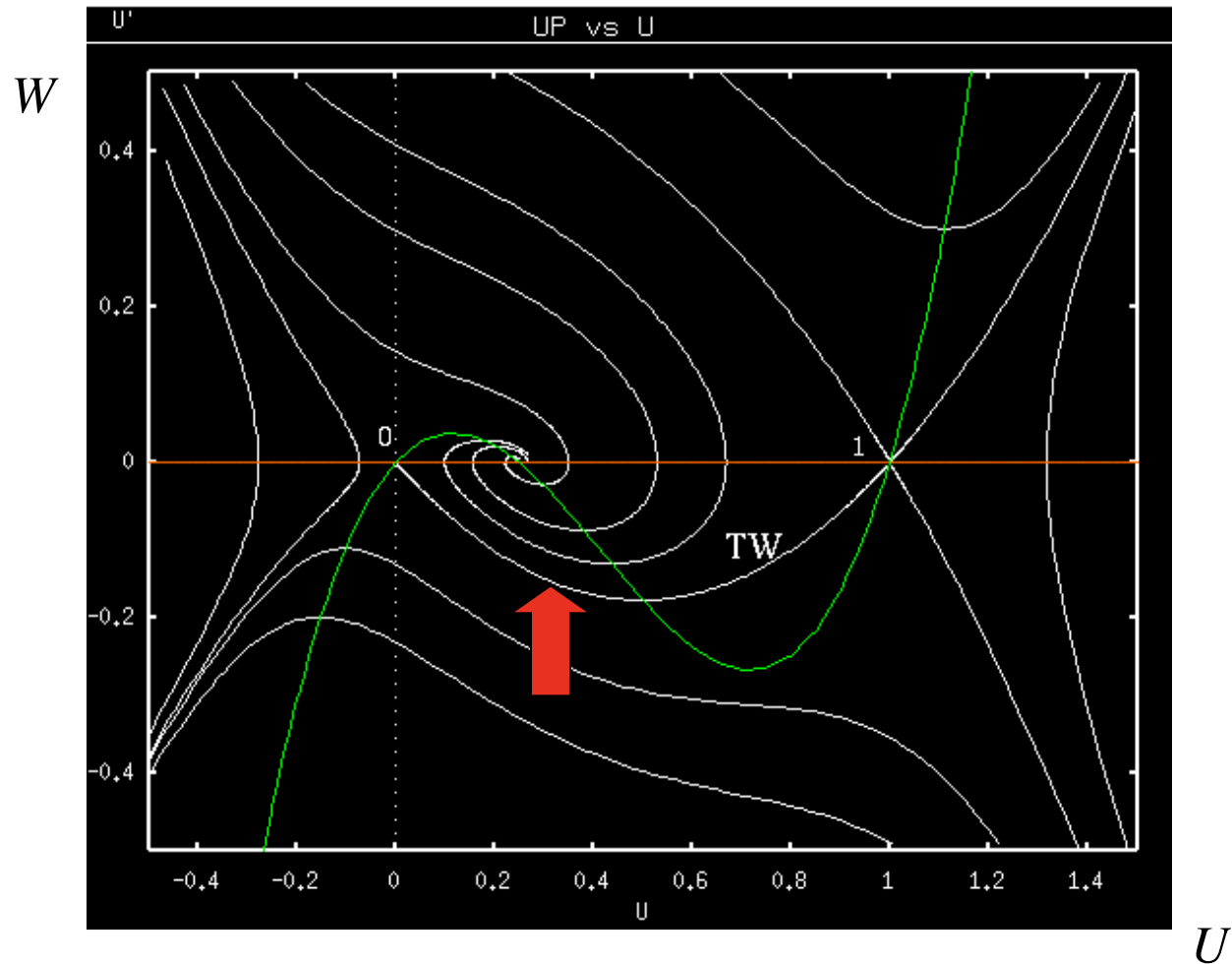
Interpretation:

Each trajectory describes how U (and W) vary as z increases over range $-\infty < z < \infty$

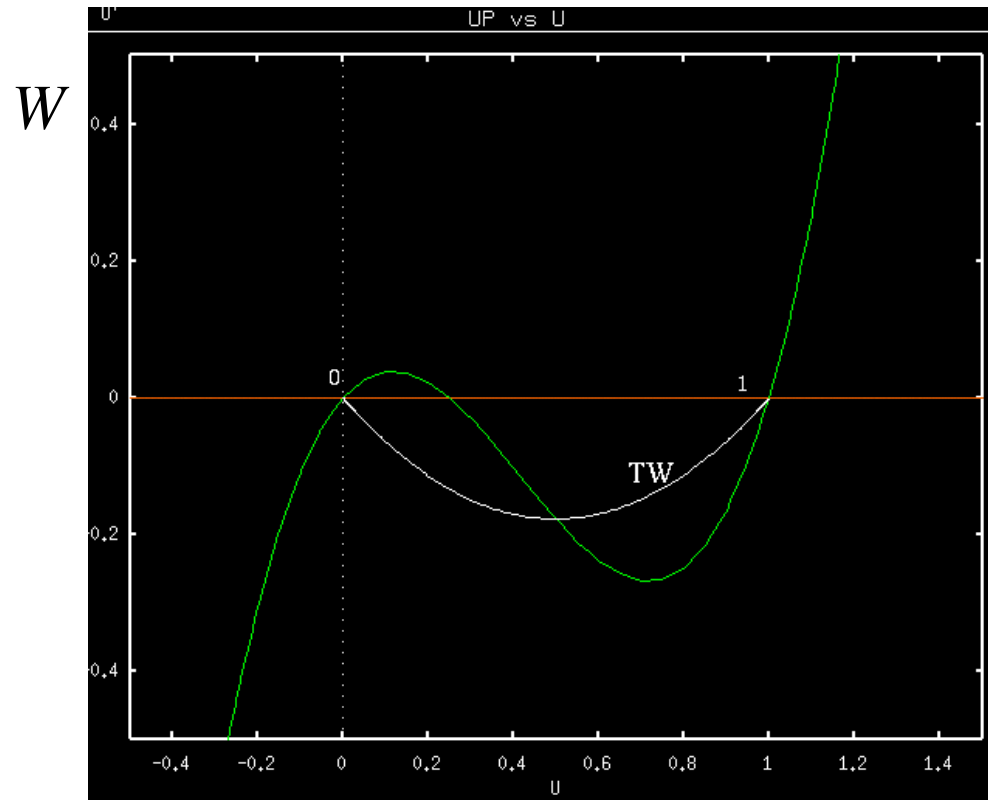
In bio applications: $u = \text{density} > 0$, so we want: a positive bounded wave: Look for a positive bounded trajectory connecting two steady states.



Here is a heteroclinic trajectory:

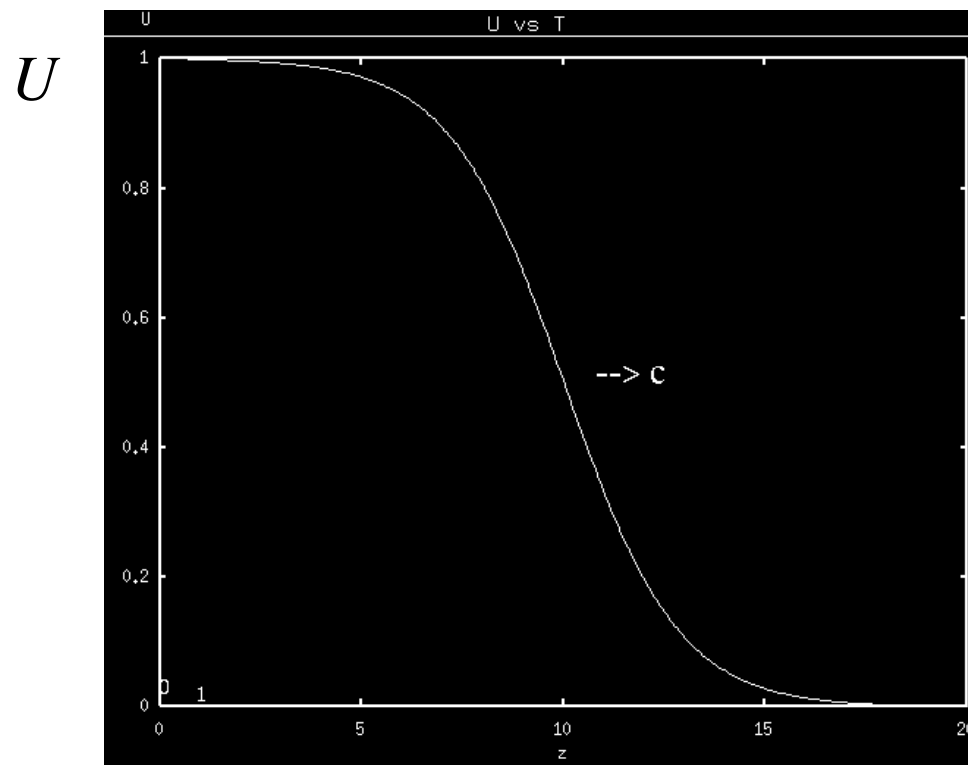


Here it is on its own:



U

And here is the shape of the wave
it represents:



z

What is the speed of the wave?

- A reaction-diffusion equation with “bistable” kinetics will admit a traveling wave that looks like a moving “front”, with high level at back, and low level ahead.
- But how fast does the wave move and does it ever stop?

There is a cute trick that allows us to answer this question for arbitrary function $f(u)$.

Determining wave speed

$$\frac{\partial u}{\partial t} = f(u) + \frac{\partial^2 u}{\partial x^2}, \quad z = x - ct$$

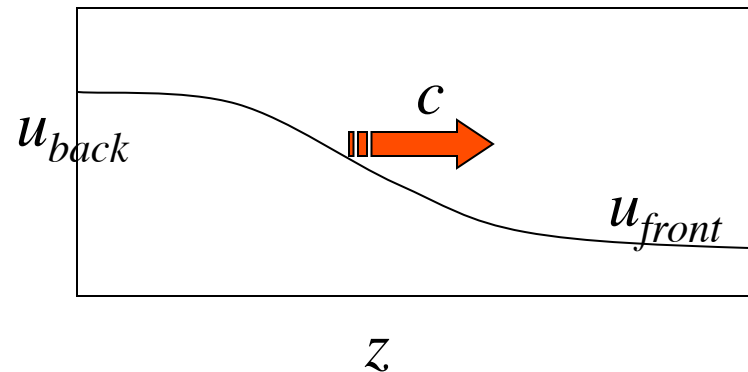
$$-c \frac{dU}{dz} - f(U) = \frac{\partial^2 U}{dz^2}$$

Multiply by dU/dz ,

$$-c \left(\frac{dU}{dz} \right)^2 - f(U) \left(\frac{dU}{dz} \right) = \frac{1}{2} \frac{d}{dz} \left(\frac{dU}{dz} \right)^2 \quad \text{integrate,}$$

$$-c \int_{-\infty}^{\infty} \left(\frac{dU}{dz} \right)^2 dz - \int_{u_{back}}^{u_{front}} f(U) dU = \frac{1}{2} \int_{-\infty}^{\infty} \frac{d}{dz} \left(\frac{dU}{dz} \right)^2 dz = 0$$

$$-c \int_{-\infty}^{\infty} \left(\frac{dU}{dz} \right)^2 dz = \int_{u_{back}}^{u_{front}} f(U) dU$$



The wave speed:

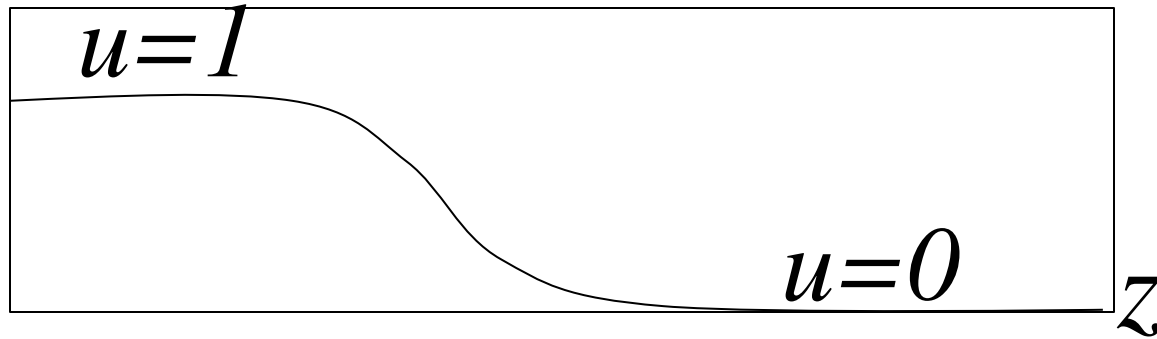
$$-c \int_{-\infty}^{\infty} \left(\frac{dU}{dz} \right)^2 dz - \int_{u_{back}}^{u_{front}} f(U) dU = \frac{1}{2} \int_{-\infty}^{\infty} \frac{d}{dz} \left(\frac{dU}{dz} \right)^2 dz = 0$$

$$-c \int_{-\infty}^{\infty} \left(\frac{dU}{dz} \right)^2 dz = \int_{u_{back}}^{u_{front}} f(U) dU$$

Finally..

$$c = - \int_{\hat{u}_{back}}^{\hat{u}_{front}} f(U) dU \bigg/ \int_{-\infty}^{\infty} \left(\frac{dU}{dz} \right)^2 dz$$

$$f(u) = u(1-u)(u - \alpha)$$



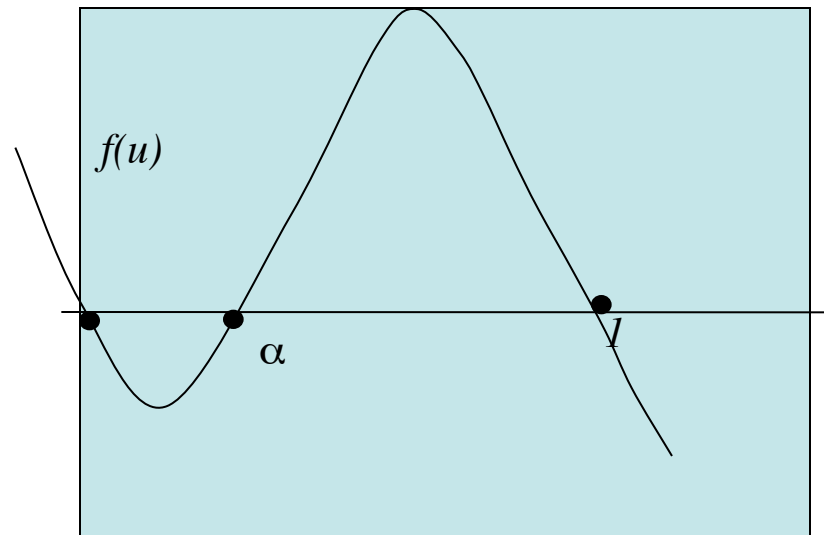
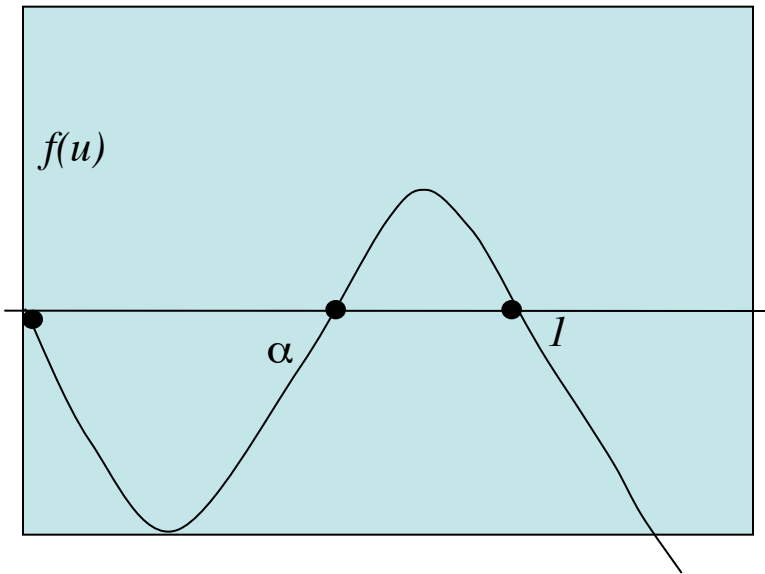
$$c = - \int_0^1 f(U) dU \bigg/ \int_{-\infty}^{\infty} \left(\frac{dU}{dz} \right)^2 dz$$

Result!

$$c = - \int_0^1 f(U) dU \bigg/ \int_{-\infty}^{\infty} \left(\frac{dU}{dz} \right)^2 dz$$

But what does this tell us????

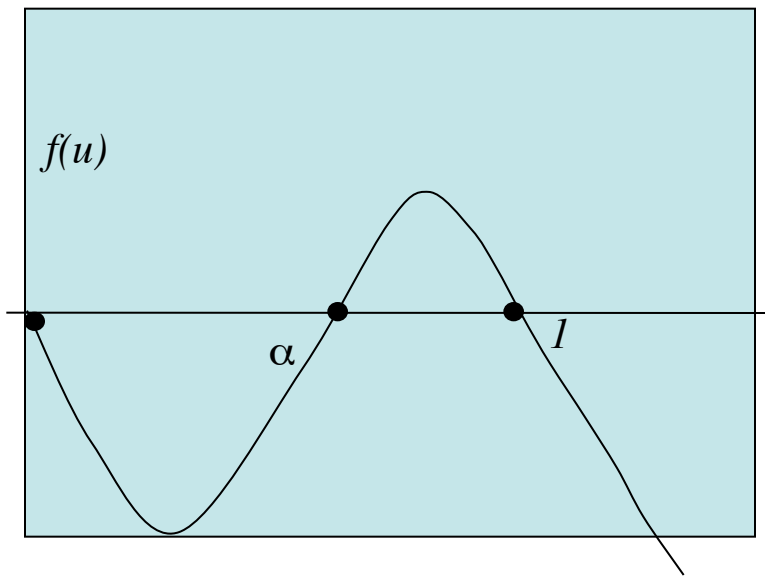
Which way does it move?



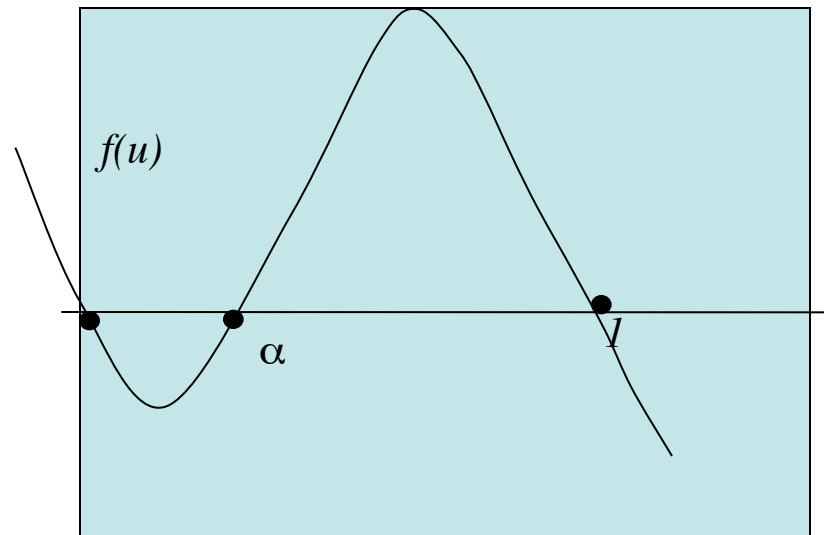
$$c = - \int_0^1 f(U) dU \bigg/ \int_{-\infty}^{\infty} \left(\frac{dU}{dz} \right)^2 dz$$

← Always positive

Which way does it move?

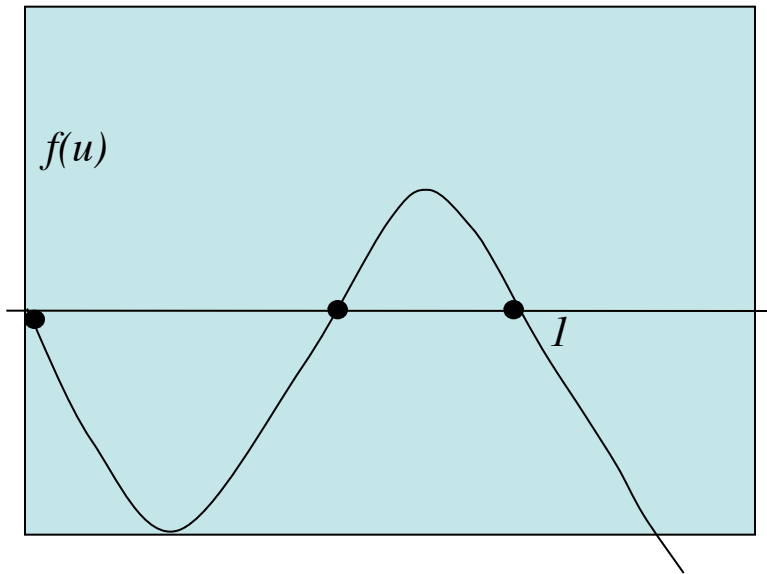


$$:- \int_0^1 f(U) dU > 0$$
$$c > 0$$

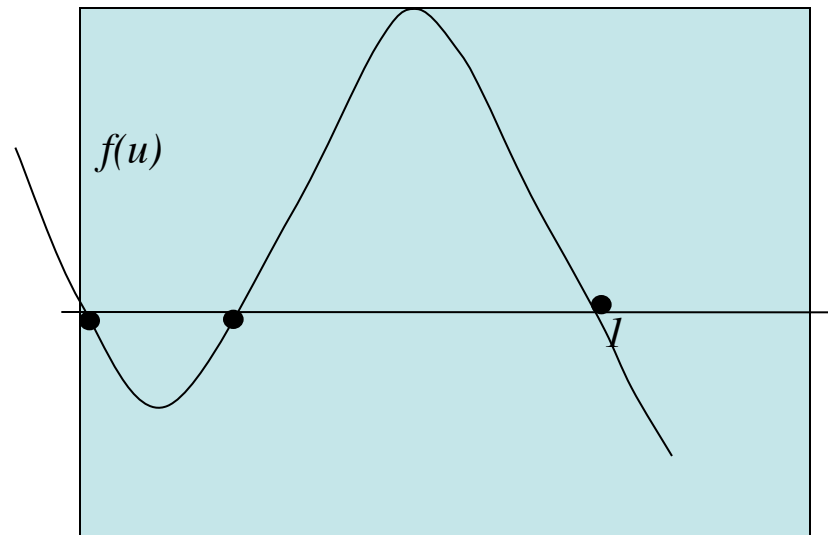


$$:- \int_0^1 f(U) dU < 0$$
$$c < 0$$

Which way does it move?

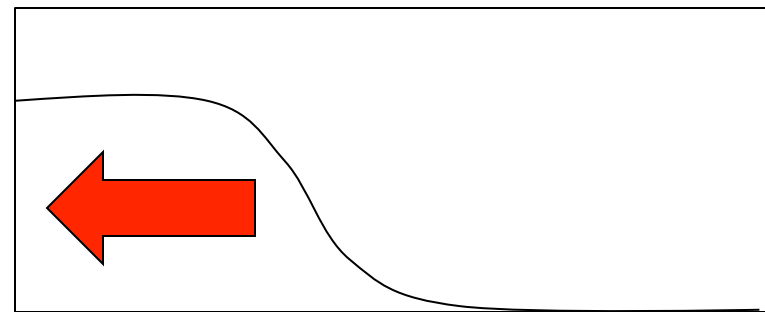
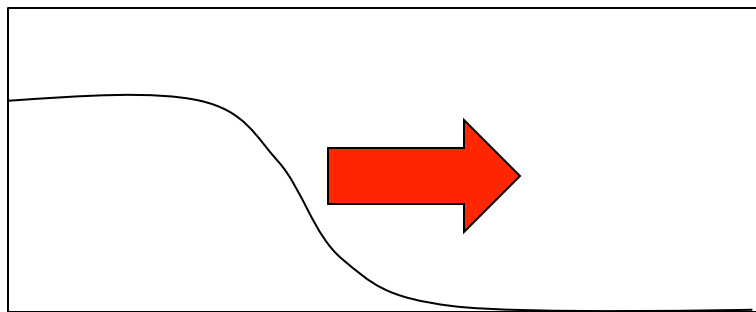
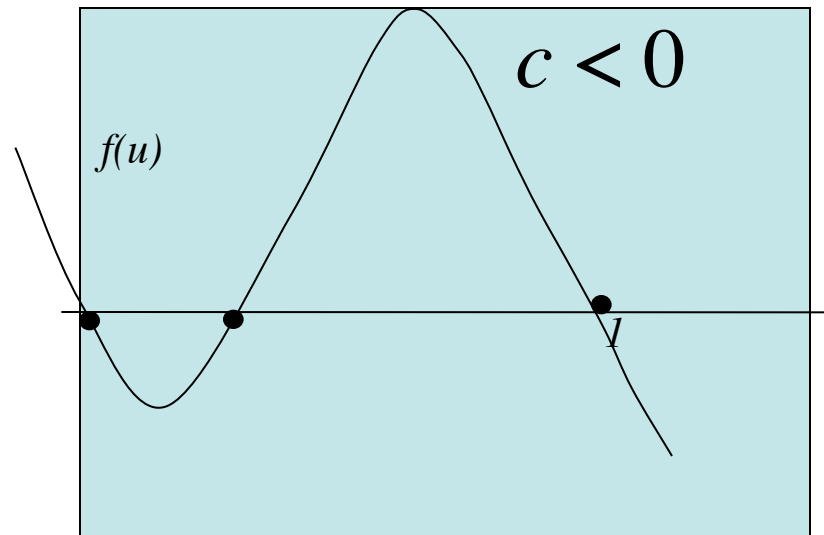
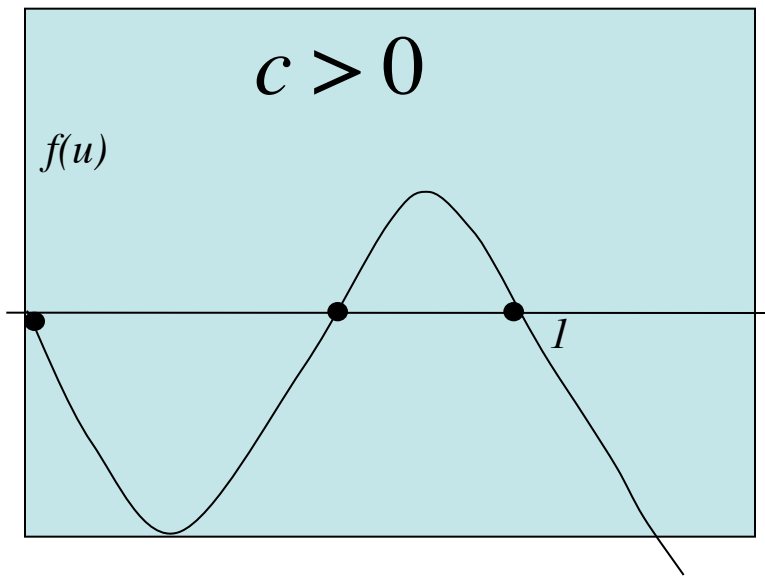


$c > 0$



$c < 0$

Which way does it move?



We can now answer the question:

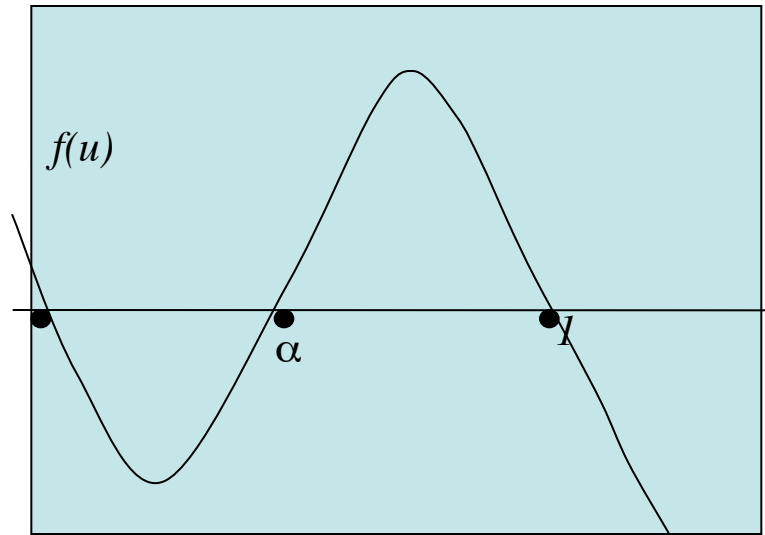
Under what conditions would
the wave stop?

Wave stops:

Speed is zero if: $0 = c = - \int_0^1 f(U) dU / \int_{-\infty}^{\infty} \left(\frac{dU}{dz} \right)^2 dz$

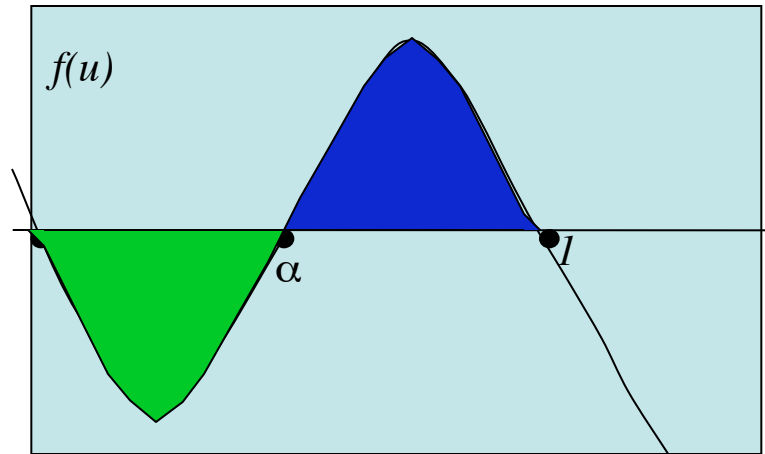
i.e.: if : $\int_0^1 f(U) dU = 0$

Geometry of stalled wave:



$$\int_0^1 f(U) dU = 0$$

Maxwell condition:



“Maxwell condition”:

$$\int_0^1 f(U)dU = 0$$

“Equal areas”

A diagram showing two shaded regions: a green inverted triangle on the left and a blue triangle on the right. The green triangle is bounded by the horizontal axis from $u=0$ to $u=\alpha$ and the curve $f(u)$. The blue triangle is bounded by the horizontal axis from $u=\alpha$ to $u=1$ and the curve $f(u)$. The areas of these two regions are equal in magnitude.

$$\int_0^{\alpha} f(U)dU = -\int_{\alpha}^1 f(U)dU$$

Can we get an explicit solution
for the wave speed?

Explicit solution?

In some special cases, e.g. $f(u)$ cubic or piecewise linear, can calculate wave speed fully by this method.

(See Keener & Sneyd p 274, Murray p 305)

For $f(u) = au(u-1)(\alpha-u) \quad 0 < \alpha < 1$

Speed of the wave is: $c = \sqrt{\frac{a}{2}}(1-2\alpha)$

$$f(u) = au(u-1)(\alpha-u) \quad 0 < \alpha < 1$$

Implications:

Wave moves right ($c > 0$) if $\alpha < 1/2$

Moves left ($c < 0$) if $\alpha > 1/2$

Wave stops ($c = 0$) precisely for one value of the parameter,
 $\alpha = 1/2$