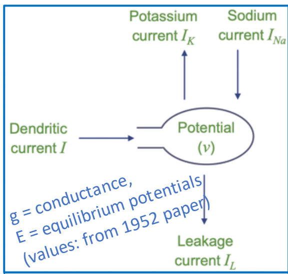
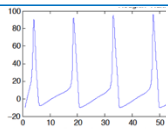


Hodgkin-Huxley model (neuron's capacitance C set to 1)

$$C\frac{dv}{dt} = -\sum_k I_k + I$$

Bio accurate but comp. expensive



$$\sum_k I_k = g_{Na} m^3 h(v - E_{Na}) + g_K n^4 (v - E_K) + g_L (v - E_L)$$

$g_K = 36$, $g_{Na} = 120$, $g_L = 0.3$

$E_K = -12$, $E_L = 10.6$, $E_{Na} = 115$

$$\frac{dm}{dt} = \alpha_m(v)(1-m) - \beta_m(v)m \qquad \alpha_m = (2.5 - 0.1v)/(e^{(2.5-0.1v)} - 1)$$

$$\frac{dn}{dt} = \alpha_n(v)(1-n) - \beta_n(v)n \qquad \alpha_n = (0.1 - 0.01v)/(e^{(1-0.1v)} - 1)$$

$$\frac{dh}{dt} = \alpha_h(v)(1-h) - \beta_h(v)h \qquad \alpha_h = 0.07e^{-v/20}$$

$$\beta_m = 4e^{-v/18} \qquad \beta_n = 0.125e^{-v/80} \qquad \beta_h = 1/(e^{(3-0.1v)} + 1)$$

LIF model

where v_r is the resting potential, I is the dendritic current, and τ and R are constants. (We'll use $\tau = 5$, $R = 1$, and $v_r = -65$mV)

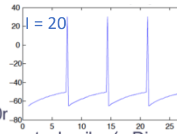
$$\tau\frac{dv}{dt} = v_r - v + RI$$

comp. inexpensive but bio inaccurate
limited repertoire of sign. behaviours

The sub-threshold (before spiking) dynamics of the sodium and potassium currents are approximated by the v_r–v term

The detailed dynamics of the spike itself are ignored. Instead, when the membrane potential reaches a threshold, we record a spike and explicitly reset the neuron

if $v \geq \vartheta$ then $v \leftarrow v_r$



A good value for the threshold ϑ is –50mV

An instantaneous value to represent the actual spike (a Dirac pulse) can be inserted immediately before the neuron is reset

Adding absolute refractory period alpha:

We simply adjust the conditions under which a spike occurs to take account of the time since the last spike

Let t_{spike} be the time of the most recent spike. Then we have

$$\text{if } v \geq \vartheta \text{ and } t - t_{spike} > \alpha \text{ then } \begin{cases} v \leftarrow v_r \\ t_{spike} \leftarrow t \end{cases}$$

Quad. IF model

$$\tau\frac{dv}{dt} = a(v_r - v)(v_c - v) + RI$$

In the absence of dendritic current, v decays to the resting potential v_r, as long as it is below a critical value v_c

But if it is above v_c it increases quickly until the neuron fires

Subthreshold profile of v modeled more accurately in QIF > LIF

Izhikevich model (2003): good compromise (no u=>QIF)

$$\frac{dv}{dt} = 0.04v^2 + 5v + 140 - u + I$$

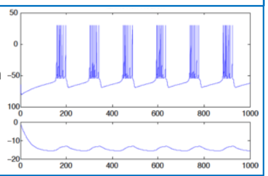
Params a,b,c,d

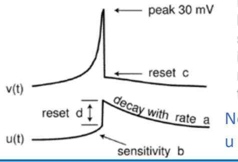
Recovery variable u

$$\frac{du}{dt} = a(bv - u)$$

$$\text{if } v \geq 30 \text{ then } \begin{cases} v \leftarrow c \\ u \leftarrow u + d \end{cases}$$

Bursting behaviour:
a=0.02, b=0.2, c=-50, d=2
Gives rise to oscillations in theta band (e.g., hippo.)



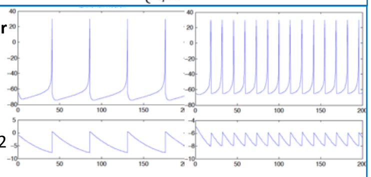


Remember that a high value for u slows the rate of increase of v, and makes it harder for the neuron to fire

Need to wait until u is down to fire

Regular spiking behaviour (excitatory):
a=0.02, b=0.2, c=-65, d=8

Fast spiking behaviour (inhibitory):
a=0.02, b=0.25, c=-65, d=2



Given $y(t)$, we can approximate the value of $y(t+\delta t)$

Euler: sensitive to dt; small dt better but comp. expensive

$$y(t + \delta t) = y(t) + \delta t\, f(y(t))$$

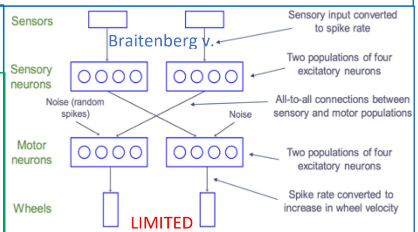
(4th order) Runge-Kutta: not as sensitive + comp. efficient

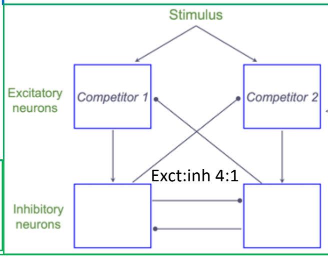
$$y(t + \delta t) = y(t) + \frac{1}{6}\delta t(k_1 + 2k_2 + 2k_3 + k_4)$$

$$k_1 = f(y(t)) \qquad k_3 = f\left(y(t) + \tfrac{1}{2}\delta t\, k_2\right)$$

$$k_2 = f\left(y(t) + \tfrac{1}{2}\delta t\, k_1\right) \qquad k_4 = f(y(t) + \delta t\, k_3)$$

Pops w/ hetero Izh neurons: add randomness to param(s) + conduction delay for every W(i,j) + constant W(i,j) + background I





WTA competition btw 2 rival resp. **to same stim** w/ mutual inhibition

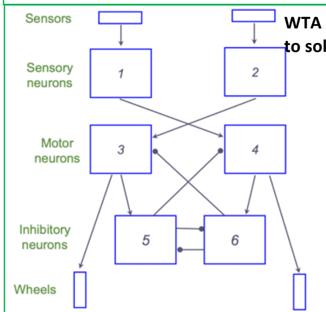
inhibits, -> excites

Bistable configuration

State where both competitors are active is **unstable**

W/ same stim, 50% of time LHS/RHS dominates. Winner based on tiny rand.diff. in firing pattern at the start of trial period. All actv dies w/o stim

WTA competition to 2 diff, competing stimuli: strongest stimulus wins most of the time. For WTA to work, needs a **lot of neurons** (800ext, 200inh): else, irregular swapping.



WTA for action selection to solve robot's dilemma

But mutual inhibition between the motor areas ensures that, when presented with equal but opposing stimuli, the robot will select one over the other, and commit to one direction to turn

For WTA to work, need **very high *a*** (Izh neurons), i.e., fast dynamics in recovery variable u: else, periodic firing where the 2 competitors are 180deg out of phase w/ each other

Connectome = description of the brain as a network (structural or functional). Structural connectome = small-world modular network.

A *network* (or graph) $G = \langle V, E\rangle$ comprises a set V of *nodes* (or vertices) and a set $E \subseteq V \times V$ of *edges* (or arcs or connections)

The relation E can also be expressed as a two-dimensional *connectivity matrix* A, such that, for all $i, j \in V$

$$A(i,j) = \begin{cases} L(i,j) \text{ if } (i,j) \in E \\ 0 \quad \text{otherwise} \end{cases}$$

$$A(j,i) = 0$$

(undirected net.) **Degree of node** k_i: num of edges it has

Network's average k: $k = \dfrac{2m}{n}$

n nodes, m edges

A *random* (or Erdős-Rényi) *network* is one in which, for every pair of nodes i and j,

$$P(A_{ij} = x) = \begin{cases} p & \text{if } x = 1 \\ 1 - p & \text{if } x = 0 \end{cases}$$

= uniform dist of randomly assigned.

Small-world network metrics, where network G = < V, E >

path length between nodes i,j: num of edges in shortest path btw nodes i,j

network's mean path length λ_G: path length avg. over all distinct pairs of nodes

clustering coefficient of node i: fraction of the set of all possible edges btw immediate neighbours of i that are actual edges (for leaf node, this is set to 1).

network's clustering coefficient γ_G **:** clustering coeff avg. over all nodes

A network G with n nodes and average degree k is a small-world network if

- it is sparse ($k << n$)
- its mean path length is comparable to that of a random network, and
- its clustering coefficient is higher than that of a random network

Small-world index

$$\sigma_G = \frac{\gamma_G / \gamma_{rand}}{\lambda_G / \lambda_{rand}}$$

It can be shown that the mean path length λ_{rand} of a random network with n nodes and average degree k is (on average) $\ln(n)/\ln(k)$ and its clustering coefficient γ_{rand} is (on average) k/n

Alternative: efficiency metrics

Watts-Strogatz Procedure to build small-world network

1) build ring lattice

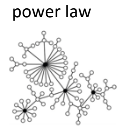
A *ring lattice* with degree k is a set of nodes notionally arranged in a circle, where each node is connected to all its (spatial) neighbours that are less than or equal to $k/2$ nodes away

2) rewire some connections

Each edge is considered in turn, and with probability p it is rewired

Rewiring an edge (j,i) means deleting (j,i) from E and adding (h,i) for some randomly chosen h

Scale-free network
k follows power law



Efficiency between neighbours i and j

Let $Eff(i,j)$ be $1/\lambda$, where λ is the path length in G from node i to node j. This captures the efficiency with which information can be propagated from i to j, the maximum being 1 if i and j are neighbours

Global efficiency

The *global efficiency* of G is then the efficiency averaged over the whole network, defined as

$$Eff_{glob}(G) = \frac{1}{n(n-1)} \sum_{i \neq j} Eff(i,j)$$

Local efficiency of a neighbourhood of a node

We can also define the efficiency of the neighbourhood of a given node

Let $G_i = \langle V', E'\rangle$ be a sub-network of G such that $V' \subseteq V$ is the set of neighbours of i, and $E' \subseteq E$ is the edges that join nodes in V'

The efficiency of the neighbourhood of node i is then $Eff_{glob}(G_i)$

The *local efficiency* of G is then the neighbourhood efficiency averaged over the whole network, defined as

$$Eff_{loc}(G) = \frac{1}{n} \sum_{i \in G} Eff_{glob}(G_i)$$

Note that if there is no path between two nodes i and j then $Eff(i,j) = 0$

Small-world index peaks when balance between global and local efficiencies

Modular network

One example is modularity. A network is *modular* if its nodes can be partitioned into subsets (*modules*, or *communities*) that

- are highly intra-connected (there are many internal connections within the module)
- but sparsely inter-connected (there are relatively fewer connections between modules)

Modular networks are typically (but not necessarily) also small-world networks

- Here's an algorithm for generating a modular network with n nodes, m edges, and C communities. Like the Watts-Strogatz procedure, it has two steps
- First, a set of C disconnected communities is created with n/C nodes each
- Each community has m/C random edges
- The second step is a rewiring process, like the Watts-Strogatz procedure again
- Each existing (intra-community) edge is considered, and with probability p is rewired as an edge between communities
- For rewired edges, the target community and target node within that community are randomly chosen

Modularity measure Q

A measure Q of how modular a given partitioning is for G is obtained by comparing the number of intra-community edges that actually occur in G with the number that would occur in a comparable network that was randomly connected

Q = (*actual fraction of edges that are within communities*) – (*expected fraction of edges that are within communities*)

In general, suppose the nodes in V are partitioned into communities, and let c_i denote the community to which node i belongs. Then we have

$$Q = \frac{1}{2m} \sum_{i,j} \left(A_{ij} - \frac{k_i k_j}{2m}\right) \delta_{c_i c_j} \; *$$

Where the 2 fractions are given as (SUM OF):

The actual fraction of intra-community edges is the sum of

$$\frac{A_{ij}}{2m}$$

In an undirected network, each edge counts twice

for all i and j in the same community, while the expected fraction of intra-community edges is the sum of

$$\frac{k_i}{2m} \times \frac{k_j}{2m}$$

The chances of an edge connecting with i and with j

for all i and j in the same community, where k_i is the degree of node i

* $\delta_{xy} = \begin{cases} 1 & \text{if } x = y \\ 0 & \text{otherwise} \end{cases}$ This function is called the Kronecker delta

Q has a maximum value of 1

Note that Q can be negative, if there are fewer connections within a "community" than there are between "communities"

-*Q* for high *p* bc more co. *between* communities than within community

The value Q is defined with respect to a given partitioning into communities

Sometimes the community structure is known in advance, so Q is easy to calculate

The modularity of a network with unknown community structure is equal to the maximum obtainable value of Q

Spatial embeddings to build modular networks: more realistic than 1D ring lattice, with each node being randomly (uniform) assigned a loc on 2D plane

By making the probability of connection depend on distance, we can construct another type of realistic network with a high small-world index, and medium to high modularity

This is not such a good model of whole-brain connectivity, but it is a good model of a small patch of cortex

Suppose the nodes are arranged on a 2D square, and each is assigned random co-ordinates in the range 0 to 0.5. This ensures that the distance between any two nodes is in the range 0 to 1 (actually less than $\sqrt{0.5}$)

Connection p btw 2 nodes

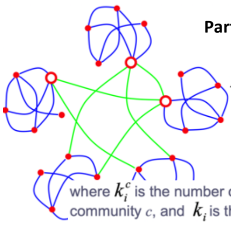
$$p = e^{-hd}$$

where d is the distance between the nodes and h is a constant

Sigma and Q *up* w/ higher h. W/ very high h, network fragments (becomes disconnected), sigma=undefined

Modular network w/ connector hub nodes or hubs

Set of hub nodes = the rich club



Participation index of node i

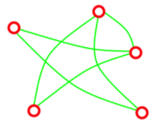
$$P_i = 1 - \sum_c \left(\frac{k_i^c}{k_i}\right)^2$$

where k_i^c is the number of edges from node i to nodes in community c, and k_i is the overall degree of node i

A node i is a *connector hub* if

- k_i is greater than the mean node degree k in the network plus the standard deviation sd of node degree in the network, and
- P_i is greater than a threshold (usually 0.3)

Connective core of network

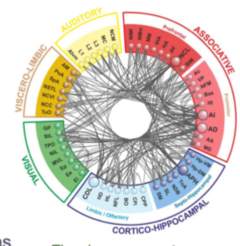


The connective core is a set of densely interconnected, topologically central nodes

Information funnels in to and fans out from the connective core

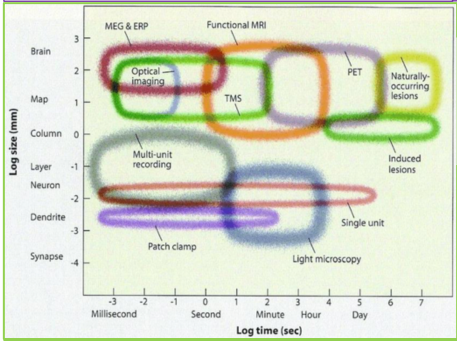
Shanahan et al. (2013)

We find a connective core in the brains of birds as well as mammals



The pigeon connectome

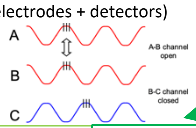
Hierarchically modular: modules also have modular structure (whole-brain human structural networks)



Measure oscillations

Theta	4-8 Hz
Alpha	8-15 Hz
Beta	15-30 Hz
Gamma	30-80 Hz

Long-range synchrony = synchronized activity at sites remote from each other (multiple surface electrodes + detectors)



w/ EEG/MEG: evidence of synchronous neuronal activity (neuron pop)

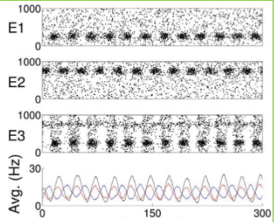
w/ intracranial electro. Spike trains whose firing rates fluctuate in time w/ each other

Functional role of sync.

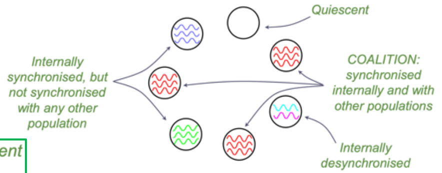
Fries: *Communication through coherence hyp.*

Sync. activity allows open/closing of channels of comm. btw pops

Competitive entrainment: E1 entrains E3 to oscillate (pattern shared from E1 to E3), to the exclusion of E2.



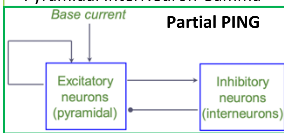
Potentially allows coalitions of processes to form, excluding rival coalitions



PING = Synch. Gamma-band oscillations (pop level)

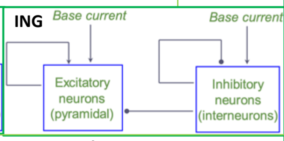
Pyramidal InterNeuron Gamma

Partial PING



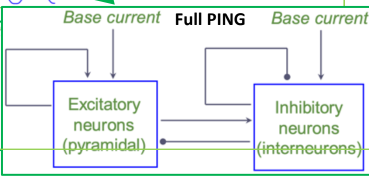
Enough for exct pop to oscillate (gamma-band)

ING



Enough for inh pop to oscillate (gamma-band) if sufficiently excited to be active w/o input of exct neurons

Full PING



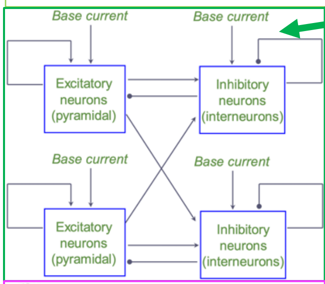
Reflects connectivity of cortex. Clear 40Hz oscillation in exct pop

For a population of neurons to exhibit synchronous gamma-band oscillation (40Hz), it is *not* necessary for individual neurons to fire regularly at 40Hz (a spike, or a burst, every 25ms)

Rather, it needs to be the case that

- there is plenty of firing in the population, and
- neurons typically only fire in a 12.5ms window

Vary conduction delay => adjust frequency of synchronous oscillation

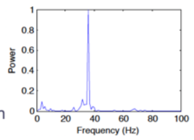


Coupled pops

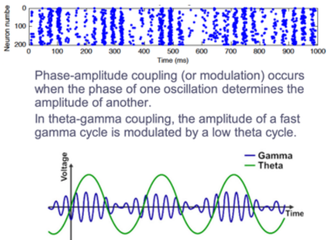
Two independent oscillating populations can be coupled by exciting each other's inhibitory neurons

With sufficient coupling strength, this can cause the populations to synchronise

Show this w/ mean firing rates or power spectrums



Theta-modulated gamma (+coupling)



Phase-amplitude coupling (or modulation) occurs when the phase of one oscillation determines the amplitude of another.

In theta-gamma coupling, the amplitude of a fast gamma cycle is modulated by a low theta cycle.

System considered to exhibit **dynamical complexity** if it balances **segregation/chaos/disorder** and **integration/synchrony/order.** Quantify using Dynamical Systems Theory and Information Theory.

State-space properties:

- Attractors
- Bifurcations
- Limit cycles

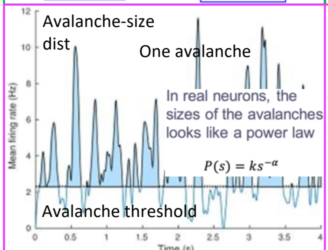
Large-scale dynamic phenomena:

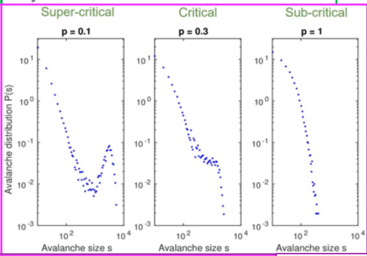
- Lyapunov stability (i.e. critical exponents)
- Spectral methods and **synchronisation**
- Phase transitions and **criticality**

System is "**critical**" if poised btw order/disorder

Often critical dynamics occur in a narrow range of some parameter (e.g. rewiring probability), with order on one side and disorder on the other --- a phase transition.

If a system's dynamics conform to a *power law*, it could suggest it is poised at criticality. Neuronal avalanches are an example.





Info/**surprise** of event w/ proba p

$$i(p) = -\log(p)$$

Entropy (bit if log2, nats if ln)

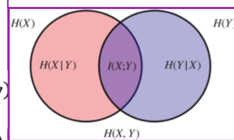
$$H(X) = -\sum_{x \in \Omega} p(x)\log_2 p(x)$$

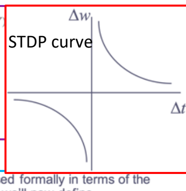
Joint Entropy

$$H(X,Y) = -\sum_{x,y} p(x,y)\log_2 p(x,y)$$

Mutual Info

$$\mathrm{MI}(X;Y) = H(X) + H(Y) - H(X,Y)$$
$$= H(X) - H(X|Y)$$





Coalition = group of modules in small-word modular network that are simultaneously active and influencing each other.

Coalition Entropy: size of the repertoire of distinct states a system can visit.

$$H_C = -\frac{1}{\log_2 |L|}\sum_{s \in L} p(s)\log_2(p(s))$$

where L is the set of distinct coalitions the system can generate and $p(s)$ is the probability of coalition s arising in any given time point.

The measure is normalised to lie to between 0 and 1.

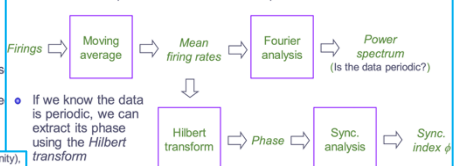
Coalition entropy Hc = measure of dynamical complexity (in oscillatory systems)

Coalition entropy is a very simple measure of dynamical complexity:

- If the system is overly integrated, every part is always synchronis (and therefore H = 0)
- If the system is overly segregated, nothing ever gets synchronise (and therefore H = 0)

Hc peaks when balance btw local/global connecti.

- Synchronisation can be assessed formally in terms of the *synchronisation index* ϕ, which we'll now define
- But this requires the extraction of the phase of the data



The instantaneous level of synchrony ϕ_c in a community c of oscillators can be quantified by

$$\phi_c(t) = \left|\left\langle e^{i\theta_k(t)}\right\rangle_{k \in c}\right|$$

more oscillators -> more accurate

where $\theta_k(t)$ is the instantaneous phase of oscillator k, $\langle\,\rangle$ denotes the average and $|\,|$ denotes the absolute value

Note that (according to the Euler formula)

$$e^{i\theta} = \cos\theta + i\sin\theta$$

In a system of N Kuramoto oscillators, the phase θ_i of oscillator i is given by

$$\frac{d\theta_i}{dt} = \omega_i + \frac{1}{N}\sum_{j=1}^{N} K_{ij}\sin(\theta_j - \theta_i - \alpha)$$

where

- ω_i is the natural frequency of the oscillator,
- α is a constant phase lag, and
- $K_{i,j}$ is the coupling strength from oscillator j to oscillator i

More precisely, if we have a set c of oscillators (a community), then the synchrony within c at time t is $\phi_c(t)$ as defined earlier. The metastability within c is the variance of the synchrony over time, given by

$$\sigma_{met}(c) = \frac{1}{T-1}\sum_{t \le T}(\phi_c(t) - \langle\phi_c\rangle_T)^2$$

where T is the number of time points and $\langle\phi_c\rangle_T$ is the mean synchrony over time

We take the mean over all communities C, to give the *metastability index* λ

$$\lambda = \langle\sigma_{met}\rangle_C$$

A time series $X(t)$ that is periodic about the origin (zero) can be mapped into the complex plane as follows

$$\zeta(t) = X(t) + iX_H(t) = A(t)e^{i\theta(t)}$$

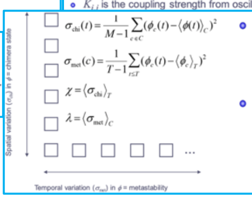
where $A(t)$ is the instantaneous amplitude of X at time t, $\theta(t)$ is the instantaneous phase of X at t, and X_H is the Hilbert transform of X at t

So, given $X_H(t)$, we have

$$\theta(t) = \tan^{-1}\left(\frac{X_H(t)}{X(t)}\right)$$

The Hilbert transform of $X(t)$ is defined as

$$X_H(t) = \frac{1}{\pi}\mathrm{P.V.}\int_{-\infty}^{\infty}\frac{X(\tau)}{t-\tau}d\tau$$



- Metastability can be quantified as the mean of the temporal variance of synchrony
- The mean of the spatial variance of synchrony says how chimera-like its states are

More precisely, we have

$$\Delta w = \begin{cases} A^+ e^{-\Delta t/\tau^+} & \text{if } \Delta t \ge 0 \\ -A^- e^{\Delta t/\tau^-} & \text{if } \Delta t < 0 \end{cases}$$

where A^+, A^-, τ^+, and τ^- are constants

Note that by varying these constants we can make the characteristic curve asymmetric

Normally $(A^-\tau^-)/(A^+\tau^+) > 1$, which prevents uncontrolled growth of w