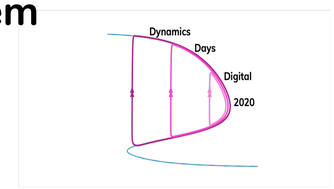
On Growth, Form, and System Dynamics: Heterochrony as a Complex System



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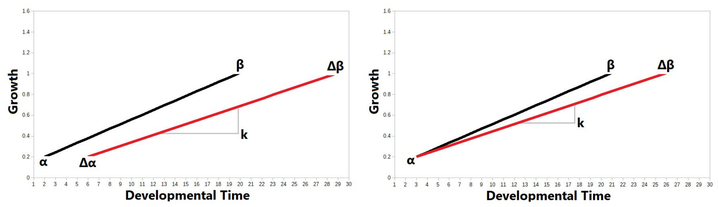
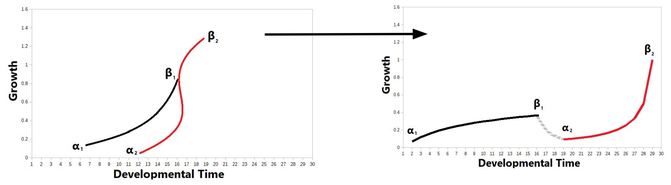
When the relative values of α and β change, the slope k changes as well. Difference between k_1 and k_2 is equivalent to τ

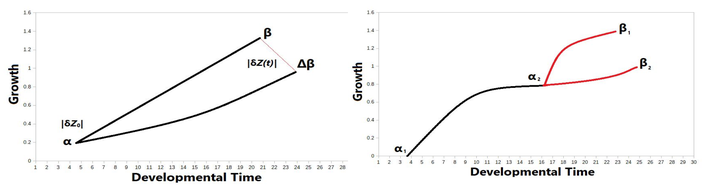


y_1 and y_2 are nominally independent ($y_1 \perp y_2$), and could represent two distinct phenotypic or genetic modules.



Δβ is determined by both a partial delay (delay in the earlier growth trajectory but not the later one) and the end of the critical period window. The rate of divergence between both growth trajectories is measured by |δZ(t)|.

For a compound trajectory (two intersecting developmental programs), the initial condition is a bifurcation point α_2 at some point in the growth trajectory rather than the initial condition α_1. In this case, we observe at least two developmental programs producing alternative growth trajectories. These growth trajectories are also linked to a common history, or the same developmental program over interval (α_1, α_2).



Growth hypothesis of heterochrony: using a linear model, the proportion of time between onset (α) and offset (β) of growth determines growth trajectory.

Review of the Alberch et.al heterochrony model. Their simple growth law can be stated as

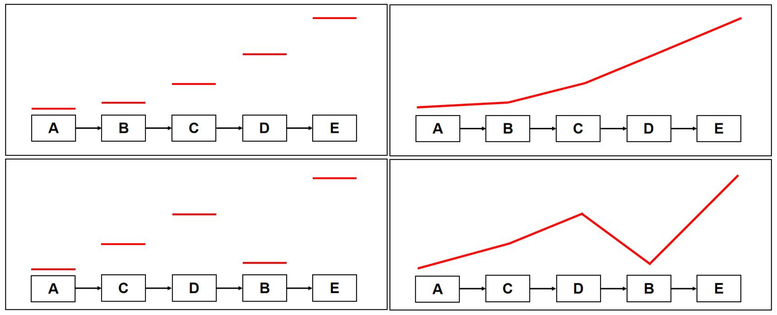
$$\frac{dy}{da} = \begin{cases} 0, & \mathrm{a} < \alpha \\ ky, & \alpha < \mathrm{a} < \beta \\ 0, & \mathrm{a} > \beta \end{cases}$$

where y grows according to

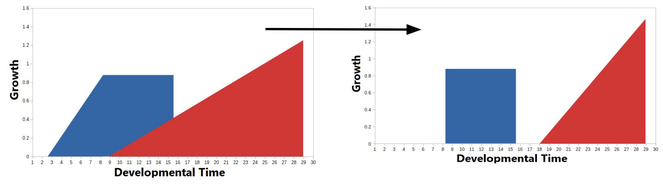
$$y(a) = y_0 e^k a$$

between onset age α and offset age β.

Sequence hypothesis of heterochrony: when the sequence of developmental events changes, so does the rate and timing of growth



Compound hypothesis of heterochrony: combination of the delay and sequence hypotheses. A continuous trajectory can become discontinuous due to specialized biological process (metamorphosis, evolutionary constraints).



Delay hypothesis of heterochrony: Delay Differential Equations (DDEs) can be used to characterize both absolute changes and relative rates of change in growth

Delay Differential Equations (DDEs) are characterized by time-delay systems. In their general form, a time-delay system is

$$\frac{d}{dt}x(t) = f(t, x(t), x_t)$$

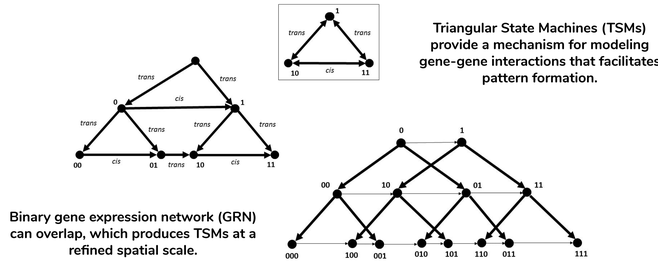
where $x_t = [x(\tau) : \tau \leq t]$ represents the trajectory of a solution in the past.

Both DDEs and time-delay systems can be solved using the method of steps. For a DDE with a single delay, the equation can be structured as

$$\frac{d}{dt}x(t) = f[x(t), x(t-\tau)]$$

We can also characterize time delays more specifically with respect to heterochrony and developmental growth trajectories. α and β can both exhibit systematic time delays (τ): $\alpha(\tau)$, $\beta(\tau)$.

Delay in the growth trajectory is characterized over the interval (α, β), and is equivalent to Δk. The total length of the delayed process is $(\beta + \tau) - (\alpha + \tau)$. Using this formulation, the rate of a delay process is k_0, the delay rate is $\frac{k_1}{k_0}$, and the length of a delay process is $\beta_x - \alpha_x$

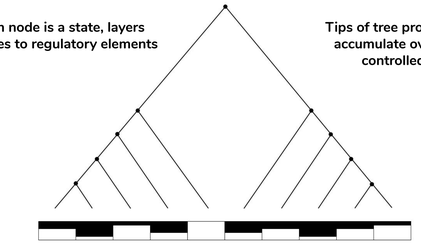


Triangular State Machines (TSMs) provide a mechanism for modeling gene-gene interactions that facilitates pattern formation.

Binary gene expression network (GRN) can overlap, which produces TSMs at a refined spatial scale.

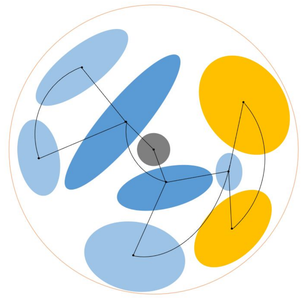
Binary tree: each node is a state, layers proceed from genes to regulatory elements

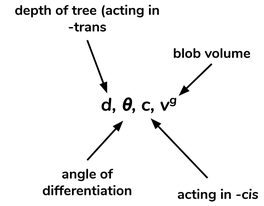
Tips of tree produce emissions that accumulate over time. Nodes are controlled by α, β, and τ



Growth by accretion across anatomical axis (A-P)

The sphericity of an embryo and GRN/TSM architecture can be visualized as an expression tree.





Each blob is a tissue at a distinct depth in the tree (color changes denote relative depth).

Check out the preprint "Developmental Incongruity as a Dynamical Representation of Heterochrony", now on *bioRxiv* (doi:10.1101/2020.07.31.231456)

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