Global asymptotic stability of solutions of nonautonomous master equations

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satisfy *Chapman-Kolmogorov equation*

$$p(x_i, t | x_j, s) = \sum_{k=1}^{n} p(x_i, t | x_k, u) p(x_k, u | x_j, s) \quad (t \geq u \geq s).$$

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- Assuming transition probabilities are of the form

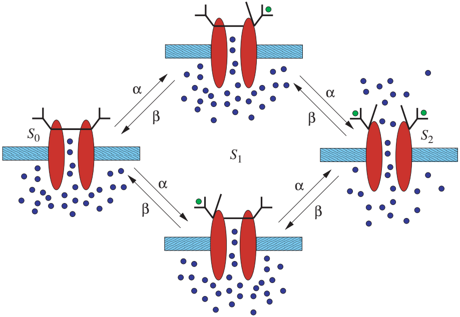
$$p(x_i, t + \Delta t|x_j, t) = a_{ij}(t)\Delta t + o(\Delta t) \quad (t \geq 0),$$

one derives *master equation* from CKE in limit $\Delta t \to 0$:

$$\frac{d\mathbf{p}}{dt} = A(t)\mathbf{p},$$

where off-diagonal entries are $a_{ij}(t) \geq 0$ and $a_{jj}(t) = -\sum_{i \neq j} a_{ij}(t)$

Ion channel with two identical subunits



- Each subunit either open or closed
    - channel has 3 states: S_0, S_1, S_2 ($i = \#$ open subunits)

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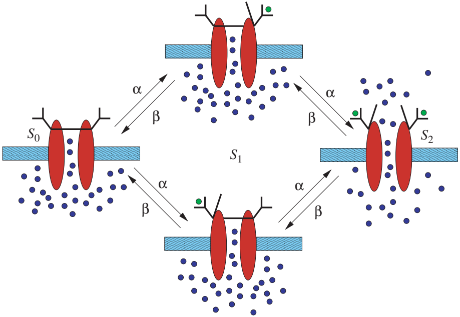

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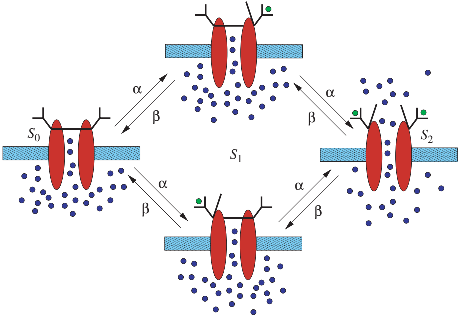

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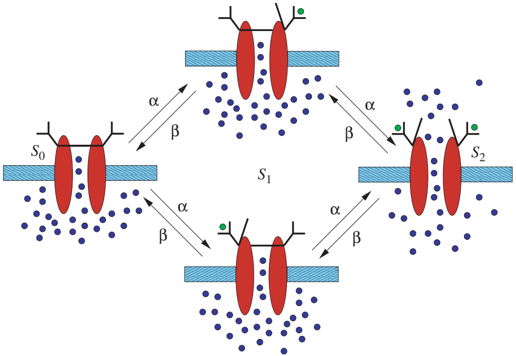
"State diagram": $S_0 \underset{\beta}{\overset{2\alpha}{\rightleftarrows}} S_1 \underset{2\beta}{\overset{\alpha}{\rightleftarrows}} S_2$

Master equation for jump process



$$S_0 \underset{\beta}{\overset{2\alpha}{\rightleftarrows}} S_1 \underset{2\beta}{\overset{\alpha}{\rightleftarrows}} S_2$$

- Let $\mathbf{p}(t) = (p_0(t), p_1(t), p_2(t))^T$ be probability distribution for $X(t)$
    - $p_i(t) = \text{Prob}\{X(t) = S_i\}$

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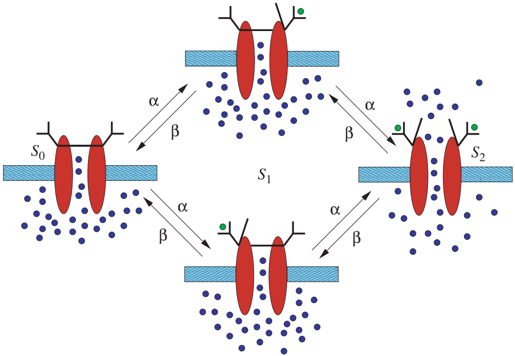

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Master equation: $$\frac{d\mathbf{p}}{dt} = A\mathbf{p} = \begin{bmatrix} -2\alpha & \beta & 0 \\ 2\alpha & -\alpha-\beta & 2\beta \\ 0 & \alpha & -2\beta \end{bmatrix} \begin{bmatrix} p_0 \\ p_1 \\ p_2 \end{bmatrix}$$

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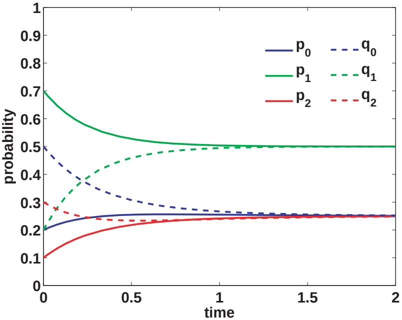
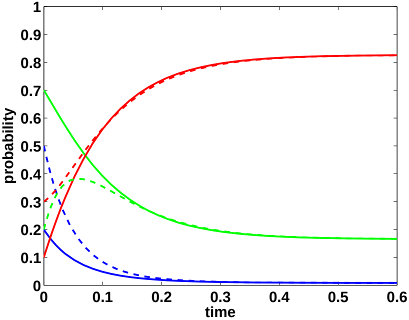


$\alpha = 10,\ \beta = 1$



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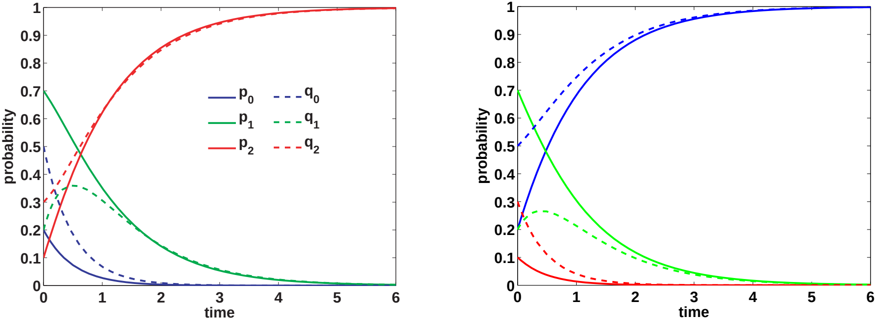
$\alpha = 1,\ \beta = 0$ $\alpha = 0,\ \beta = 1$



van Kampen's theorem for autonomous master equations

Theorem

Suppose A is a constant $\mathbb{W}$-matrix. If A is neither decomposable nor splitting, then every probability distribution solution of the master equation approaches a unique stationary distribution.

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A is *decomposable* if there exists permutation matrix P such that

$$P^{-1}AP = \begin{bmatrix} A_1 & 0 \\ 0 & A_2 \end{bmatrix}$$

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- Zero is repeated eigenvalue iff $\mathbb{W}$-matrix is decomposable or splitting

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- Every probability distribution solution $\mathbf{p}$ of master equation is of form

$$\mathbf{p}(t) = \mathbf{v}_1 + c_2 e^{\lambda_2 t}\mathbf{v}_2 + \cdots + c_n e^{\lambda_n t}\mathbf{v}_n$$

  where $\mathbf{v}_i$'s are corresponding eigenvectors and c_i's are polynomials in t of degree $< n$

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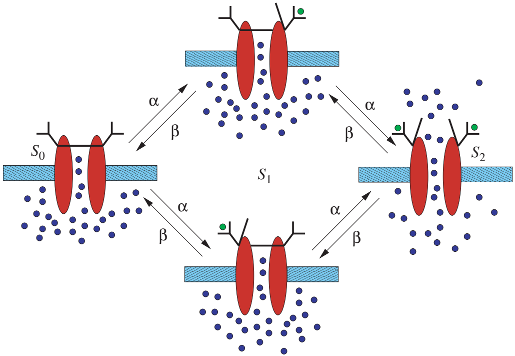
- Therefore, $\mathbf{p}(t) \to \mathbf{v}_1$ independent of initial conditions

Nonautonomous master equation



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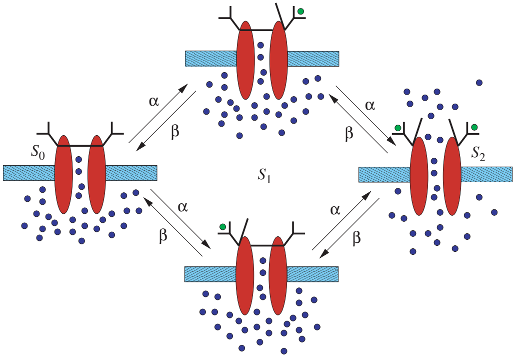

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- Ion channel kinetics are dependent on *external* factors such as membrane voltage $\Rightarrow \alpha, \beta$ are functions of time!
- How will solutions behave now?

Behavior of solutions of nonautonomous master equation

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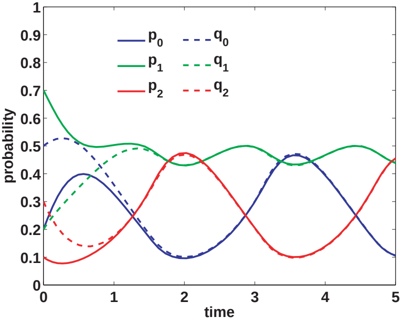
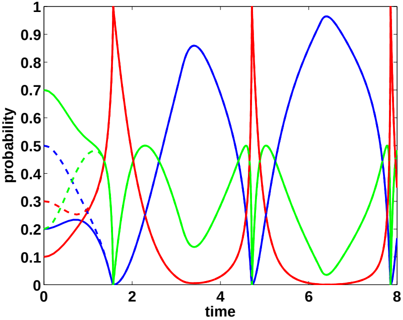
$\alpha = |\sin(t)|$, $\beta = |\cos(t)|$



$\alpha = |\tan(t)|$, $\beta = t$



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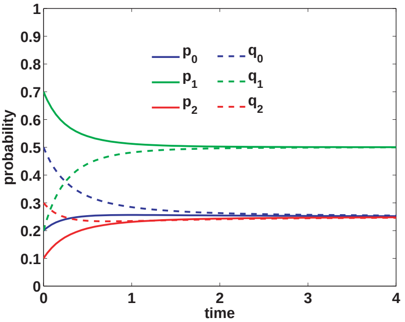
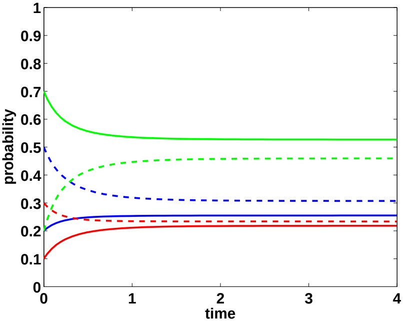
$\alpha = \beta = (t+1)^{-1}$



$\alpha = \beta = \exp(-2t)$



What causes solutions to approach each other?

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Example:

$$\begin{aligned} a_{11}(t) &= -1 - 9\cos^2(6t) + 12\sin(6t)\cos(6t) \\ a_{12}(t) &= 12\cos^2(6t) + 9\sin(6t)\cos(6t) \\ a_{21}(t) &= -12\sin^2(6t) + 9\sin(t)\cos(6t) \\ a_{22}(t) &= -1 - 9\sin^2(6t) - 12\sin(6t)\cos(6t) \end{aligned}$$

$A(t) = [a_{ij}(t)]$ has eigenvalues -1 and -10 for all $t \geq 0$, yet

$$\mathbf{x}(t) = e^{2t}\begin{bmatrix} 2\sin(6t) + \cos(6t) \\ 2\cos(6t) - \sin(6t) \end{bmatrix} + 2e^{-13t}\begin{bmatrix} 2\cos(6t) - \sin(6t) \\ 2\sin(6t) - \cos(6t) \end{bmatrix}$$

is a solution of $\dot{\mathbf{x}} = A(t)\mathbf{x}$

Current theory

If the transition rates vary according to specific functions of time, the concentration of each subunit state approaches to a specific function of time (in comparison to a constant value when transition rates are constant) regardless of the initial concentration of states.

Nekouzadeh, Silva and Rudy, *Biophys J* (2008)

$\mathcal{L}^1$-norm as Lyapunov function for H_0-solutions

- Recall $||\mathbf{x}||_1 = \sum_{i=1}^{n} |x_i|$

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$$\frac{d||\mathbf{x}(t)||_1}{dt} = -\sum_{i\in[n]\setminus I_+} \sum_{j\in I_+} a_{ij}(t)x_j(t) - \sum_{i\in[n]\setminus I_-} \sum_{j\in I_-} a_{ij}(t)\,|x_j(t)| - \sum_{i\in I_-} \sum_{j\in I_+} a_{ij}(t)x_j(t) - \sum_{i\in I_+} \sum_{j\in I_-} a_{ij}(t)\,|x_j(t)|$$

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- If $\frac{d||\mathbf{x}(t)||_1}{dt} = 0$ then $A(t)$ is decomposable or splitting ($\Rightarrow \lambda_2(t) = 0$)
- Converse: if $\Re(\lambda_2(t)) < 0$ then $\frac{d||\mathbf{x}(t)||_1}{dt} < 0$

Conjecture

$$\text{Master equation:} \quad \frac{d\mathbf{p}}{dt} = A(t)\mathbf{p} \tag{1}$$

Conjecture

Let $A : \mathbb{R}_+ \to \mathbb{R}^{n\times n}$ be a continuous, $\mathbb{W}$-matrix-valued function, and let $\lambda_1(t), \ldots, \lambda_n(t)$ be an ordering of the n eigenvalues of $A(t)$, counting multiplicities, such that $0 = \lambda_1(t) \geq \Re(\lambda_2(t)) \geq \cdots \geq \Re(\lambda_n(t))$ for all $t \geq 0$. If $\Re(\lambda_2)$ is not integrable, then all probability distribution solutions of (1) are globally asymptotically stable (GAS); i.e., given any two probability distribution solutions $\mathbf{p}$ and $\mathbf{q}$ of (1),

$$\mathbf{p}(t) - \mathbf{q}(t) \to \mathbf{0} \quad \text{as} \quad t \to \infty.$$

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- If $\Re(\lambda_2(t)) < 0$ then $\frac{d||\mathbf{x}(t)||_1}{dt} < 0$ for any H_0-solution $\mathbf{x}(t)$
- The nonintegrability of $\Re(\lambda_2)$ "should" ensure that $||\mathbf{x}(t)||_1 \to 0$

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- Theorem can be extended slightly using similar proof

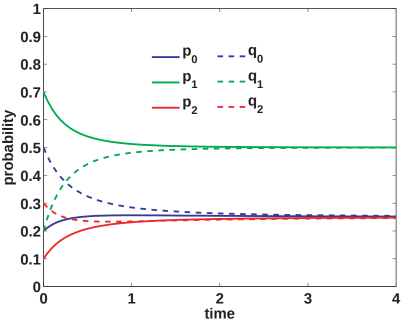
Theorem

Suppose $A(t) = f(t)M$ for all $t \geq 0$, where M is constant $\mathbb{W}$-matrix and $f : \mathbb{R}_+ \to \mathbb{R}_+$ is continuous. Then probability distribution solutions of the master equation are GAS if and only if M is neither decomposable nor splitting and f is not integrable.

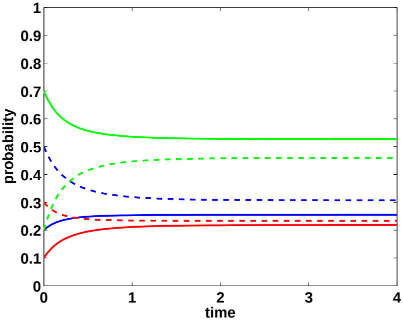
Example of first generalization

$$\frac{d\mathbf{p}}{dt} = A\mathbf{p} = f(t)\begin{bmatrix} -2 & 1 & 0 \\ 2 & -2 & 2 \\ 0 & 1 & -2 \end{bmatrix}\mathbf{p}$$

$$f(t) = (t+1)^{-1}$$



$$f(t) = \exp(-2t)$$



Generalization of van Kampen's theorem for asymptotically periodic A

Theorem

If A is continuous, $\mathbb{W}$-matrix-valued and there exists a continuous, periodic, $\mathbb{W}$-matrix-valued function B whose ω-limit set contains at least one matrix that is neither decomposable nor splitting such that

$$\lim_{t \to \infty} ||A(t) - B(t)||_1 = 0,$$

then probability distribution solutions of the master equation are GAS.

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then probability distribution solutions of the master equation are GAS.

- Idea: $\mathcal{L}^1$-norm must decrease by some uniform amount during each period of B.
- Special case of conjecture since λ_2 asymptotically approaches a nonpositive periodic function which is negative at least once during each period.

Another generalization of van Kampen's theorem

Theorem

If A is differentiable, $\mathbb{W}$-matrix-valued function such that both A and its derivative are bounded, and the ω-limit set of A contains no matrix which is either decomposable or splitting, then probability distribution solutions of the master equation are GAS.

Another generalization of van Kampen's theorem

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If A is differentiable, $\mathbb{W}$-matrix-valued function such that both A and its derivative are bounded, and the ω-limit set of A contains no matrix which is either decomposable or splitting, then probability distribution solutions of the master equation are GAS.

- Idea: if $||\mathbf{x}(t)||_1 \to r > 0$, then $\omega(A)$ contains a decomposable or splitting matrix

Another generalization of van Kampen's theorem

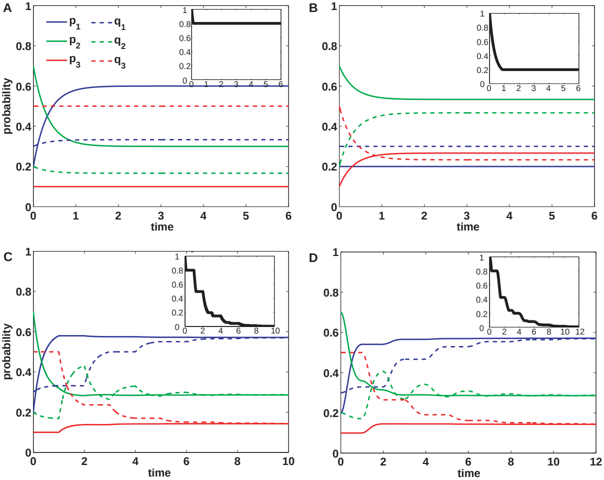
Theorem

If A is differentiable, $\mathbb{W}$-matrix-valued function such that both A and its derivative are bounded, and the ω-limit set of A contains no matrix which is either decomposable or splitting, then probability distribution solutions of the master equation are GAS.

- Idea: if $||\mathbf{x}(t)||_1 \to r > 0$, then $\omega(A)$ contains a decomposable or splitting matrix
- Special case of conjecture since
  - $\omega(\lambda_2)$ is nonempty and contains negative number
  - $\lambda_2'(t)$ is bounded

$\lambda_2(t) = 0$ for all $t \geq 0$ but solutions are GAS

$$A(t) = \begin{cases} A_1, & t \in [0,1), \\ A_2, & t \in [1,2), \end{cases}, \quad A_1 = \begin{bmatrix} -1 & 1 & 0 \\ 1 & -1 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \quad A_2 = \begin{bmatrix} 0 & 0 & 0 \\ 0 & -1 & 1 \\ 0 & 1 & -1 \end{bmatrix}$$



Thank you!

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