Asymptotic behaviour of the run and tumble equation for bacterial chemotaxis

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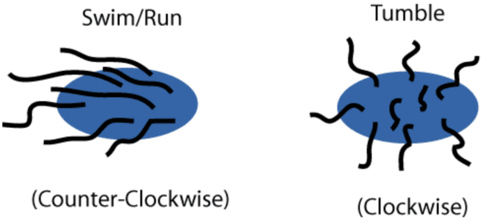
Run and Tumble Equation - Behaviour

- Run: Travel in a straight line
- Tumble: Instantaneous change velocity
  - Post-tumbling velocity is uniform on a ball
  - Example: *E. Coli* [Berg, Brown '72]
- Tumbling rate λ: s.t. bacteria jumps faster when it goes away from high chemical concentration
- $\implies$ Bias in velocity towards high concentrations of chemoattractant
- $\implies$ In long-time: Aggregation of bacteria



[1]

[1] https://www.mit.edu/ kardar/teaching/projects/chemotaxis(AndreaSchmidt)

Run and Tumble Equation - Introduction

Run and Tumble Model for Chemotaxis - [Stroock '74, Alt '80]

$$\partial_t f = \mathcal{L}[f] = -v \cdot \nabla_x f + \int_{\mathbb{R}^d} \int_{\mathcal{V}} \lambda(m')\kappa(v,v') f(t,x,v') - \lambda(m) f(t,x,v)$$
$$f(0,x,v) = f_0(x,v) \in \mathcal{P}(\mathbb{R}^d, \mathcal{V}) \tag{RT}$$

where $x \in \mathbb{R}^d$ and $v \in \mathcal{V} = B(0, V_0)$ so that $|\mathcal{V}| = 1$.

- $f(t,x,v) \geq 0$ density of bacteria
- $\lambda(m) : \mathbb{R} \to [0,\infty)$ tumbling rate,
  $\mathbb{P}\,(\text{Tumble happens in } [t, t+\Delta t]) = \lambda(v_t \cdot \nabla_x M(x_t))\Delta t + \mathcal{O}(\Delta t)$.
- $m = v \cdot \nabla_x M$, M : external signal,
- $M = m_0 + \log(S)$, $m_0 > 0$, S : chemoattractant concentration,
- Probability distribution of change in $v \to v'$: $\int_{\mathcal{V}} \kappa(v,v')\,\mathrm{d}v' = 1$.
- Tumbling frequency
  $T(x,v,v') = \lambda(m')\kappa(v,v') = 1 - \chi\psi(x,v')$, $\chi \in (0,1)$

- Fixed $S(x) \rightsquigarrow$ (RT) is a linear equation.
- Studied in [Othmer-Hillen SIAP '00-'02]
- [CRS KRM '15]: $\exists!$ stationary state & exponential convergence in $d = 1$ for $\psi(x, v) = -\mathrm{sgn}(x \cdot v)$, $\chi \in (0, 1)$.
- [Mischler-Weng KRM '17]: Extension to $d \geq 1$ for $\psi(x, v) = -\mathrm{sgn}(\partial_t S + v \cdot \nabla_x S)$ & $S(x)$ radially symmetric.
- Realistic case: (RT) + Poisson like coupling

$$-\Delta S + \alpha S = \rho(t, x) := \int_{\mathcal{V}} f(t, x, v)\, \mathrm{d}v. \qquad \text{(P)}$$

- [Bournaveas-Calvez ANIHPC '09]: $\exists$ critical mass & blow up phenomena ($d = 2$, spherically symmetric initial data)
- [Calvez JEMS '19]: Nonlinear couplings, $\exists$ travelling wave solutions, $d = 1$ (complements the experimental observations).

Run and Tumble Equation - We study... & Motivation

- Linear case with $\psi(m) = \text{sgn}(m)$ & ψ Lipschitz ($d \geq 1$).
- Non-linear toy model *(weakly non-linear)*:

$$S(x) = S_\infty(x)(1 + \eta N(x) * \rho), \quad \rho(t,x) = \int_{\mathcal{V}} f(t,x,v)\,\mathrm{d}v, \quad \text{(NL)}$$

  where $\eta > 0$ a small constant, N a compactly supported positive smooth function, S_∞ a smooth function.
    - Intermediate case
    - S can be considered as a perturbation of the linear equation when $N * \rho$ is decreasing and η small.
- Parabolic scaling: $\tau = \varepsilon^2 t$, $\xi = \varepsilon t \to$ as $\varepsilon \to 0$ aggregation-diffusion equation on the spatial density ρ:

$$\partial_\tau \rho = \nabla_\xi \cdot (\nabla_\xi \rho - u_c(\xi)\rho) \;\text{ where } u_c = \xi \int_{\mathcal{V}} v' \psi(v' \cdot \nabla_x M(\xi))\,\mathrm{d}v'.$$

- (RT) with (P) $\rightsquigarrow$ Keller-Segel (Chemotactic wave paradox)
- FLKS - Saturation of the cell velocity $\rightsquigarrow u_c = h(|\nabla S|)$. [Dolak-Schmeiser '05]

- Extension of the most recent result [Mischler, Weng 2017] on the linear equation to dimension $d \geq 1$ by getting rid of the radial symmetry assumption on $S(x)$ also for smooth ψ.
- Introducing the weakly non-linear model
  - Build a unique stationary solution
  - Exponential convergence towards the stationary solution
- Constructive proofs.
- Convergence rates are quantifiable.
- Convergence results are in weighted TV norms with exponential weights, i.e. $e^{-\gamma M} = S^{-\gamma}$, $\gamma > 0$ small constant.
- Providing perspectives to treat the more realistic non-linear couplings.

(H1) Distribution of the change in velocity due to tumbing is uniform.

$$\kappa \equiv 1.$$

(H2) Tumbling rate increases as the bacteria move away from the regions with higher density of chemoattractant.

$$\lambda(m) = 1 - \chi\psi(m), \quad m = v' \cdot \nabla_x M, \, \chi \in (0,1),$$

where ψ is a bounded, odd, increasing function, $\|\psi\|_\infty \leq 1$ and $m\psi(m)$ is differentiable.

(H3) Chemoattractant density decreases as $|x| \to \infty$.

- $M(x) \to -\infty$ as $|x| \to \infty$,
- $\exists R \geq 0$ and $m_* > 0$ s.t. when $|x| > R$, $|\nabla_x M(x)| \geq m_*$.
- $\text{Hess}(M)(x) \to 0$ as $|x| \to \infty$ and $\text{Hess}(M)(x)$ is bounded.

(H4) $\exists\tilde{\lambda} > 0$ (dep. on $\psi, \|\nabla_x M\|_\infty$) and $\exists k) > 0$ (dep. on ψ)

$$\int_{\mathcal{V}} m'\psi(m')\,\mathrm{d}v' \geq \tilde{\lambda}|\nabla_x M(x)|^k.$$

- If $\psi(x) = \mathrm{sgn}(z)$ then $k = 1$ and

$$\tilde{\lambda} = \int_{-V_0}^{V_0} |v_1|(V_0^2 - v_1^2)^{(d-1)/2} \frac{\pi^{(d-1)/2}}{\gamma((d-1)/2+1)}.$$

- If ψ is differentiable with $\psi'(0) > 0$ then $k = 2$ and $\tilde{\lambda}$ depends on the exact form of ψ.

Intuition: Analogy with the kinetic equations

- Lower bound in the collision frequency.
- Bound on the confinement term.

Theorem (Linear case - J. Evans, H. Y., arXiv:2103.16524, 2021)

Suppose that $t \mapsto f_t$ *is the solution to* (RT) *with* $f_0 \in \mathcal{P}(\mathbb{R}^d \times \mathcal{V})$ *and that (H1)-(H4) are satisfied.*

- *There exist* $C, \rho > 0$ *(indep. from* f_0*) such that*

$$\|f_t - f_\infty\|_* \leq Ce^{-\sigma t}\|f_0 - f_\infty\|_*, \qquad (\bigstar)$$

where f_∞ *is the unique steady state solution of* (RT) *and*

$$\|\mu\|_* = \int_{\mathbb{R}}^d \int_{\mathcal{V}} \Psi(m, \psi(m)) e^{-\gamma M(x)} |\mu| \, \mathrm{d}v \, \mathrm{d}x.$$

- *If there exist* $C_1, C_2, \alpha > 0$ *such that*

$$C_1 - \alpha\langle x\rangle \leq M(x) := \log(S(x)) \leq C_2 - \alpha\langle x\rangle,$$

then $(\bigstar)$ *holds with* $\|\mu\|_{**} = \int_{\mathbb{R}}^d \int_{\mathcal{V}} e^{\delta\langle x\rangle}|\mu| \, \mathrm{d}v \, \mathrm{d}x$, *where* σ *is a constant small enough dep. on* M *and* $\langle x\rangle := \sqrt{1+|x|^2}$.

Theorem (Non-linear c. - J. Evans, H. Y., arXiv::2103.16524, 2021)

Suppose that $t \mapsto f_t$ *is the solution to* (RT)-(NL) *which is given by*

$$S(x) = S_\infty(x)(1 + \eta N(x) * \rho), \quad \rho = \int f_t \, \mathrm{d}v,$$

where N *is a smooth function with a compact support,* $\eta > 0$ *a small constant and* S_∞ *is a smooth function satisfying for* $C_1, C_2, \alpha > 0$

$$C_1 - \alpha\langle x\rangle \leq M_\infty(x) := \log(S_\infty(x)) \leq C_2 - \alpha\langle x\rangle,$$

where $\langle x\rangle := \sqrt{1 + |x|^2}$. *Suppose also that (H1)-(H4) are satisfied and* ψ *is a Lipschitz function.*

- *There exists* $\tilde{C}$ *(dep. on* C_1, C_2, α*) s.t. if* $\eta < \tilde{C}$ *there exists a unique steady state solution* f_∞ *to* (RT)-(NL).
- *Any* f_0 *satisfying* $\|f_0\|_{**} \leq K$ *(*K *dep. on* $\sigma, \chi, V_0, \eta, \cdots$*) then we have*

$$\|f_t - f_\infty\|_{**} \leq C e^{-\sigma t/2} \|f_0 - f_\infty\|_{**}. \qquad (\star\star)$$

Sketch of the proof - Linear case

- Proof is given by Harris's Theorem [Harris 1956] (Ergodicity of Markov Processes). Mass- & positivity-preserving linear semigroup

  (M) Uniform mixing property in a region
  "Minorisation condition"
  (FL) Geometric drift condition
  "Foster-Lyapunov condition"
  $\Bigg\} \Longrightarrow \Bigg\{$ ∃! stationary state; Exp. convergence

- Adjoint operator
  $\mathcal{L}^*[\phi] = v \cdot \nabla_x \phi + \lambda(v \cdot \nabla_x M) \left(\int_{\mathcal{V}} \phi(x, v') \, \mathrm{d}v' - \phi(x, v) \right)$
  - (FL): Find $\gamma, D > 0$ and ϕ such that $\boxed{\mathcal{L}^* \phi \leq -\gamma \phi + D}$.
- $(\mathcal{T})_{t \geq 0}$: $\partial_t f + v \cdot \nabla_x M + \lambda(x, v) f = 0$ and $\mathcal{J}[f] := \int_{\mathcal{V}} \lambda' f' \, \mathrm{d}v'$

(M): $$\boxed{f_t = \mathcal{S}_t f_0 = \mathcal{T}_t f_0 + \int_0^t \mathcal{T}_{t-s} \left(\mathcal{J} f_s \right) \mathrm{d}s.}$$

Sketch of the proof - Non-linear case

- Build a stationary solution
  - $S = S_\infty(1 + \eta N * \rho) \rightsquigarrow S$ can be considered as a perturbation of the linear equation when $N * \rho$ is decreasing and η small.
  - Fixed point argument: $G(M) = \log\big(S_\infty(1 + \eta N * \rho^M)\big)$, $\rho^M = \int f_\infty^M \, \mathrm{d}v'$.
- Contraction argument
  - $f = \mathcal{L}_{M_t} f = \mathcal{L}_{\tilde{M}} f - (\mathcal{L}_{\tilde{M}} - \mathcal{L}_{M_t}) f, \quad \tilde{M}$ fixed point of G.

$$\boxed{f_t = \mathcal{S}_t^{\tilde{M}} f_0 + \int_0^t \mathcal{S}_{t-s}^{\tilde{M}} (\mathcal{L}_{\tilde{M}} - \mathcal{L}_{M_s}) f_s \, \mathrm{d}s.}$$

$$\|f_t - f_\infty\|_{**} = \|\mathcal{S}_t^{\tilde{M}} f_0 - f_\infty\|_{**} + \left\| \int_0^t \mathcal{S}_{t-s}^{\tilde{M}} (\mathcal{L}_{\tilde{M}} - \mathcal{L}_{M_s}) f_s \, \mathrm{d}s \right\|_{**}$$

Intuition for the toy model

- Aim: Find steady states for (RT) coupled with $-\Delta S + S = \rho$.
- Idea: Schauder fixed point arg. on $G(M) = \log S$ s.t. $-\Delta S + S = \rho^M$, ρ^M is the spatial density of (RT) with fixed M.
- Aim: Find sufficient bounds on $\int\int f^M \phi \, \mathrm{d}x \, \mathrm{d}v$ to run Schauder arg. (compact, convex set of S)
- Need: Tightness of ρ^M (for compactness) $\rightsquigarrow$ moment estimates.
- We know $S \sim e^{-\alpha\langle x \rangle}$.
- Foster-Lyapunov: $\int e^{\alpha\gamma\langle x \rangle}\rho \leq C$ with $\gamma < 1$.
- Consider

$$
\begin{aligned}
-\Delta S + S &= \rho_* + \eta\rho, \\
-\Delta S + S &= \rho_*(1 + \eta\rho) \implies S = N * (\rho_*(1 + \eta\rho)), \\
S &= S_\infty(1 + \eta N * \rho),
\end{aligned}
$$

  N positive smooth function, S_∞ smooth function, $\eta > 0$.
- Retain the idea of fixed point argument on the chemoattractant.

Thank you!