

Multi-class oscillating systems of interacting neurons

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The main motivation is to find a good **microscopic model** to describe **oscillating biological systems**, mostly neurons.

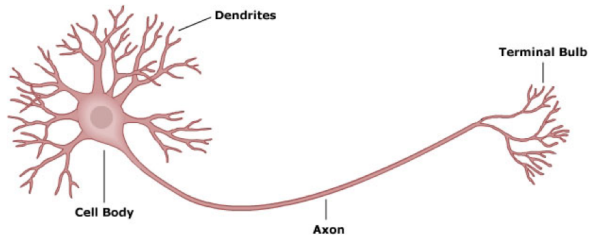
We will consider large systems of interacting point processes presenting intrinsic oscillations in large scale, although single neuron's dynamics do not encode any oscillatory behavior.

In other words : we try to answer to the following question : **How does periodic behavior emerge at a macroscopic level when the single units do not have any tendency to behave periodically ?**

Outline

- 1 Introduction of the model : Point process models for large systems of interacting neurons given by Hawkes processes.
- 2 Propagation of chaos for a particular multi-class system.
- 3 Erlang kernels allow to develop the memory. Associated Piecewise Deterministic Markov Process (PDMP).
- 4 Study of the oscillatory behavior of the limit system.
- 5 And of the finite size system \implies Large deviations.

Neurons



- Neurons : generate and propagate **action potentials** the long of their axons.
- They communicate by transmitting **spikes** : this is a fast transmembrane current of K^+ / Na^+ -ions, stimulated by ion pumps.

Closer look to spikes

The shape and the time duration of spikes is almost deterministic - and always “the same” (for a fixed neuron, under the same experimental conditions)

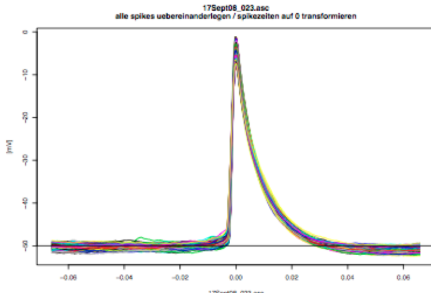
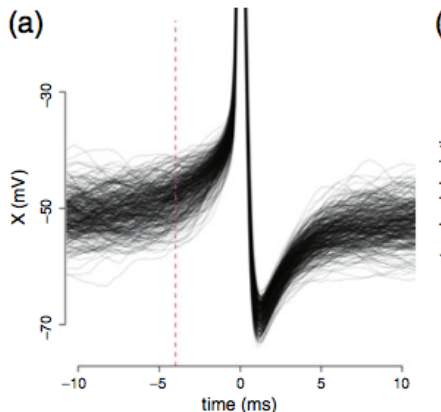


FIGURE: Picture by R. Höpfner, Mainz

The next picture is by Jahn, Berg, Hounsgaard, Ditlevsen, 2011. It also shows that spikes **do not appear** when the membrane potential hits a fixed threshold...



- The duration of each spike is very short (about 1 ms) - followed by a **refractory period** during which the neuron can not spike again (about 1 ms).
- Since shape of spike almost deterministic \rightarrow report if at a given time there is **presence or absence of a spike** \rightarrow **spike trains**.
- We do this in continuous time.

Point processes

- **Point process model** : for each neuron, we model the random times of appearance of a spike.
- N neurons (= point processes) which interact.
- Counting process associated to neuron i , $1 \leq i \leq N$:

$Z_i(t)$ = number of spikes of neuron i during $[0, t]$.

- Spike counting process associated to neuron i : $Z_i(t)$ has **intensity process** $\lambda_i(t)$ defined by

$$P(Z_i \text{ has a jump during }]t, t + dt] | \mathcal{F}_t) = \lambda_i(t)dt.$$

- We will use **Hawkes intensities** : intensity $\lambda_i(t)$ incorporates the **interactions between the neurons**.
- It also represents the way the spiking behavior of a neuron depends on its history :
It is commonly admitted that spike trains should be processes having **infinite or variable memory**.
- Hence $\lambda_i(t)$ is a **stochastic process, depending on the whole history before time t** .

Interacting Hawkes processes

- Intensity of i -th neuron given by

$$\lambda_i(t) = f_i \left(\sum_{j=1}^N \int_{]0,t[} h_{ij}(t-s) dZ_j(s) \right)$$

↑ rate fct ↑ loss fct ↑ past event

- $f_i =$ **spiking rate function** of neuron i . $f_i : \mathbb{R} \rightarrow \mathbb{R}_+$, increasing, *Lipschitz*.

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- If h_{ij} is not of compact support, then : **truly infinite memory process**.

Example

$$\lambda_i(t) = f_i \left(\sum_j \int_{]0,t[} W_{ij} e^{-\alpha_i(t-s)} dZ_j(s) \right)$$

- $W_{ij} =$ *synaptic weight* of neuron j on neuron i . If $W_{ji} > 0$, then the synapse is **excitatory**, if $W_{ji} < 0$, then it is **inhibitory**.
- $e^{-\alpha_i(t-s)}$: past events are forgotten at exponential speed.
- Neurons which have a direct influence on the spiking activity of i are those belonging to

$$\mathcal{V}_i := \{j : W_{ij} \neq 0\} \Rightarrow \text{Interaction graph.}$$

Hawkes intensity

- *Hawkes processes are very popular nowadays and widely used :*
 - *in neuroscience : Hansen, Reynaud-Bouret and Rivoirard (2015), Julien Chevallier (2016), ...*
 - *in genomics : Reynaud-Bouret and Schbath (2006), ...*
 - *in financial econometrics : Jaisson and Rosenbaum (2014), ...*
- *have been introduced in 1971 by Hawkes to model earthquakes and the appearance of their aftershocks.*
- *Main idea : Self exciting (influencing) point processes : past events trigger future events.*
- *For linear Hawkes processes, there is a representation via an equivalent **branching process**.*

Discussion of the model

-

$$X_i(t) := \sum_j \int_{]0,t[} h_{ij}(t-s) dZ_j(s) :$$

can be interpreted as **membrane potential** of neuron i at time t .

- **Integrate-and-fire model** : the membrane potential of neuron i collects all the past spike events of its *presynaptic neurons*. The neuron fires depending on the height of its actual membrane potential, at rate $f_i(X_i(t))$. (*Warning : in the literature, the name "Integrate-and-fire"-model is often reserved to diffusion models.*)

Multiclass systems of interacting neurons

Multi-class framework :

- Our system is made of n **populations** or clusters of neurons $k = 1, 2, \dots, n$. This number n is **fixed** throughout the talk.

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- Our system is made of n **populations** or clusters of neurons $k = 1, 2, \dots, n$. This number n is **fixed** throughout the talk.
- Each population k consists of N_k **neurons** described by their counting processes

$$Z_{k,i}(t), 1 \leq i \leq N_k.$$

- Within a population, all neurons behave in the same way. **This is a mean-field assumption.**

- Intensity of any neuron belonging to population k :

$$\lambda_k(t) = f_k \left(\frac{1}{N_{k+1}} \sum_{1 \leq j \leq N_{k+1}} \int_{]0,t[} h_k(t-s) dZ_{k+1,j}(s) \right).$$

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- **Very particular interaction graph** : Population k only influenced by population $k + 1$.

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Mean field limit

- What happens in the large system size limit ?
- I.e. $N = N_1 + \dots + N_n$ total number of neurons $\rightarrow \infty$ such that for each population

$$\lim_{N \rightarrow \infty} \frac{N_k}{N} > 0.$$

- Remember the intensity of population k

$$\lambda_k(t) = f_k \left(\int_{]0,t[} h_k(t-s) \left[\frac{1}{N_{k+1}} \sum_{1 \leq j \leq N_{k+1}} dZ_{k+1,j}(s) \right] \right)$$

$$\uparrow \text{ LLN} \rightarrow d\mathbb{E}(\bar{Z}_{k+1}(s)),$$

where \bar{Z}_{k+1} is the counting process of a typical neuron belonging to population $k+1$ in the $N \rightarrow \infty$ -limit.

Limit system

- Limit system : family of counting processes $\bar{Z}_k(t)$, $k = 1, \dots, n$, solution of an **inhomogeneous equation**

$$\bar{Z}_k(t) = \int_0^t \int_{\mathbb{R}_+} \mathbf{1}_{\{z \leq f_k(\int_0^s h_k(s-u) d\mathbb{E}(\bar{Z}_{k+1}(u))\}} N^k(ds, dz),$$

where N^k , $k = 1, \dots, n$ are independent PRM on $\mathbb{R}_+ \times \mathbb{R}_+$ with intensity $d s d z$.

- Existence of a pathwise unique solution of the limit system standard under **Lipschitz assumption on the f_k** ; follows ideas of Delattre, Fournier and Hoffmann (2016) on high-dimensional Hawkes processes in the one-population case.

Convergence to limit system

- Convergence of the finite size system (of the **collection of empirical measures of each population**) to the limit : standard as well : We take empirical measures within each population and obtain

Theorem (Propagation of chaos, Ditlevsen and L. 2017)

$$\left(\frac{1}{N_1} \sum_{1 \leq i \leq N_1} \delta_{(Z_{1,i}^N(t))_{t \geq 0}}, \dots, \frac{1}{N_n} \sum_{1 \leq i \leq N_n} \delta_{(Z_{n,i}^N(t))_{t \geq 0}} \right) \\ \rightarrow \mathcal{L}((\bar{Z}_1(t), \dots, \bar{Z}_n(t))_{t \geq 0})$$

in probability, as $N \rightarrow \infty$. ($\mathcal{P}(D(\mathbb{R}_+, \mathbb{R}_+))$ is endowed with the weak convergence topology ass. with the Skorokhod top. on $D(\mathbb{R}_+, \mathbb{R}_+)$.)

- Multi-population frame : reminiscent of Graham (2008), see also Graham and Robert (2009) : coined the notion of “multi-chaoticity” .
- Note that in the limit the different populations are independent.
Interactions of classes do only survive in law.

Study of intensities of the limit system

- Taking expectations yields : $m_t^k = \mathbb{E}(\bar{Z}_k(t))$, $k = 1, \dots, n$, solves

$$\frac{dm_t^k}{dt} = f_k \left(\int_0^t h_k(t-u) dm_u^{k+1} \right).$$

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- Equations depending on the whole history.
- Hawkes processes are truly infinite memory processes - the intensity depends on the whole history.
- We will present situations, in which these limit intensities $\frac{dm_t^k}{dt}$ **OSCILLATE!** We do this in the case where the system can be completed to a system of ODE's.

Developing the memory

- Consider **Erlang memory kernels** :

$$h_k(t) = c_k \frac{t^{\eta_k}}{(\eta_k)!} e^{-\nu_k t}, \nu_k > 0, \eta_k \in \mathbb{N}_0, c_k \in \mathbb{R}.$$

- The delay of influence of the past is **distributed**. It takes its maximum at about η_k/ν_k time units back in the past.
- The higher the order of the delay η_k , the more the delay is concentrated around its mean value $(\eta_k + 1)/\nu_k$.
- If $c_k > 0$, then the influence of pop $k + 1$ on pop k is excitatory, else : inhibitory.

Recall : Limit integrated intensities given by

$$m_t^k = \mathbb{E}(\bar{Z}_k(t)), k = 1, \dots, n,$$

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CLAIM : In case of Erlang memory kernels h_k , it is possible to **complete** (x^1, \dots, x^n) to a **higher dimensional system of ODE's!!!!** This is a standard trick in delay equations that I am going to explain now.

Developing the memory - continued

- Suppose e.g. $h_k(t) = h(t) = c_k t e^{-\nu_k t}$ (short memory of length 1).

$$h'(t) = -\nu_k h(t) + c_k e^{-\nu_k t}$$

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- In terms of the intensity process : Introduce for $1 \leq k \leq n$,

$$x_t^k = \int_0^t h_k(t-s) dm_s^{k+1}, \quad y_t^k = \int_0^t h_1(t-s) dm_s^{k+1}(s).$$

\Rightarrow two dimensional system of ODE's

$$\dot{x}_t^k = -\nu_k x_t^k + y_t^k,$$

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where the last equation is linked to the next population.

Summary

- memory kernels of type $h_k(t) = c_k t e^{-\nu_k t}$ give rise to a $2n$ -dimensional system of coupled ODE's which are of type

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for $1 \leq k \leq n$.

- Increasing the delay of the memory kernel will increase the dimension of this system of coupled ODE's.
- This can be restated in terms of the original finite size jump process

Associated system of PDMP's

Let

$$X^{k,1}(t) = \frac{1}{N_{k+1}} \sum_{j=1}^{N_{k+1}} \int_{]0,t[} h_k(t-s) dZ_{k+1,j}(s), 1 \leq k \leq n,$$

and complete to system $X^{k,i}, 1 \leq k \leq n, 1 \leq i \leq \eta_k + 1$: PDMP with generator

 $A\varphi(x) =$

$$\sum_{k=1}^n \left[\sum_{i=1}^{\eta_k} \left\{ -\nu_k x^{k,i} + x^{k,i+1} \right\} \frac{\partial \varphi}{\partial x^{k,i}} - \nu_k x^{k,\eta_k+1} \frac{\partial \varphi}{\partial x^{k,\eta_k+1}} \right] + \sum_{k=1}^n N_{k+1} f_{k+1}(x_{k+1,1}) \left[\varphi\left(x + \frac{c_k}{N_{k+1}} e_{k,\eta_k+1}\right) - \varphi(x) \right].$$

Some simulations in the case of a single neuron

A single neuron's spike train represented by a Hawkes process with an Erlang memory kernel, of memory order 3 :

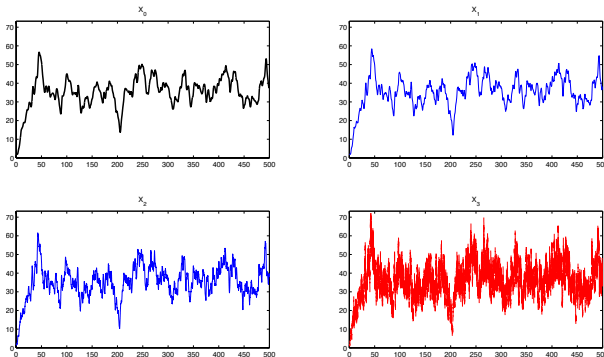


FIGURE: Picture by Aline Duarte, Sao Paulo

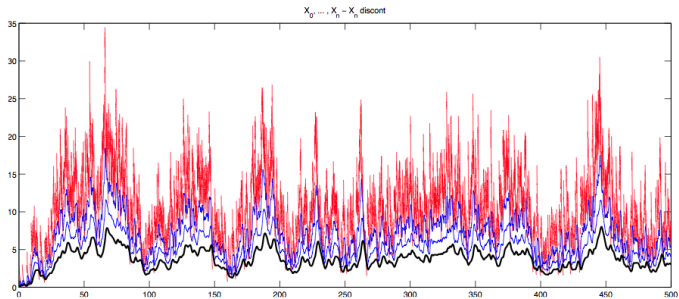


FIGURE: Picture by Aline Duarte

Monotone cyclic feedback systems

- Recall we wanted to find oscillations for the limit intensities.
- Our system of coupled ODE's in case of memory of order 1 : For $1 \leq k \leq n$,

$$\dot{x}_t^k = -\nu_k x_t^k + y_t^k, \quad \dot{y}_t^k = -\nu_k y_t^k + c_k f_{k+1}(x_t^{k+1}).$$

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- This system is a **monotone cyclic feedback system** (Mallet-Paret and Smith 1990).
 - Cyclic means : population k is only influenced by population $k + 1$, for all k .
 - Feedback : population n is influenced by population 1.
 - Monotone : all rate functions f_k are non-decreasing.

- Put $\delta := \prod_{k=1}^n c_k$. If $\delta > 0$, the system is of positive feedback, else, it is of negative feedback.

- Put $\delta := \prod_{k=1}^n c_k$. If $\delta > 0$, the system is of **positive feedback**, else, it is of **negative feedback**. We will consider the **negative feedback case**.

Suppose that $f_k, 1 \leq k \leq n$, are bounded analytic Lipschitz functions and that the system is of negative feedback. Then :

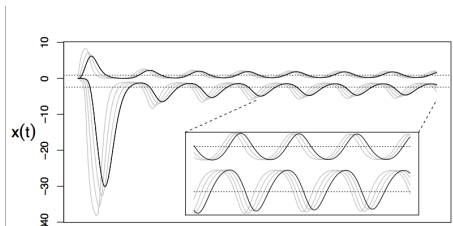
Theorem (Mallet-Paret and Smith)

- 1) $\exists!$ *equilibrium point x^* of the above system.*
- 2) \exists *easily verifiable condition implying that x^* is unstable. In this case, there exists at least one – but not more than a finite number of – non constant periodic orbits. One of them is attracting.*

Remark

So here they are, the oscillations (not for the m_t^k , but for the intensities)! Because : non constant periodic orbit = oscillations

Simulation of a system with 2 populations and memory 3 for the first population and memory 4 for the second one :



The role of the order of the memory

Definition

We call order of the memory of population k the index $\eta_k \in \mathbb{N}$ such that

$$h_k(t) = c_k \frac{t^{\eta_k}}{(\eta_k)!} e^{-\nu_k t}.$$

We call “total order of memory of the system” the number $\kappa := n + \sum_{k=1}^n \eta_k$.

Proposition (Hopf bifurcation due to increasing memory)

Suppose that $\nu_k = 1$, for all $1 \leq k \leq n$. Then there exists κ^* such that for all $\kappa < \kappa^*$, the equilibrium point x^* is stable. For $\kappa \geq \kappa^*$, the systems presents oscillations.

So increasing the DELAYS pushes the system towards oscillations.

Central limit Theorem

We have well understood the behavior of the limit system

*To which extent does the large time behavior of the limit system (m_t^1, \dots, m_t^n) **predict** the large time behavior of the finite size system ???*

\Rightarrow CLT where convergence of both N and t to infinity is considered. Under suitable assumptions on the way $N, t \rightarrow \infty$: depends on spectral properties of offspring matrix.

Diffusion approximation of the intensity process

Second answer to : **To which extent are the oscillations of the limit system also felt by the finite size system ?** :

Have a look at the “Large intensity-small jump size”-diffusion approximation (in case $n = 2$ and $\eta_1 = \eta_2 = 1$) :

Recall the generator of the associated PDMP :

$$\begin{aligned}
 A\varphi(x) = & \\
 & \sum_{k=1}^2 \left[\{-\nu_k x^{k,1} + x^{k,2}\} \frac{\partial \varphi}{\partial x^{k,1}} - \nu_k x^{k,2} \frac{\partial \varphi}{\partial x^{k,2}} \right] \\
 & + \sum_{k=1}^2 N_{k+1} f_{k+1}(x_{k+1,1}) \left[\varphi\left(x + \frac{c_k}{N_{k+1}} e_{k,2}\right) - \varphi(x) \right].
 \end{aligned}$$

Small jumps of size $\frac{c_k}{N_{k+1}}$ appearing at rate $N_{k+1} f_{k+1} \Rightarrow$

$$\left\{ \begin{array}{l} dX_1(t) = -\nu_1 X_1(t)dt + Y_1(t)dt \\ dY_1(t) = -\nu_1 Y_1(t)dt + c_1 f_2(X_2(t))dt \\ \quad + \frac{c_1}{\sqrt{N_2}} \sqrt{f_2(X_2(t))} dB_2(t) \end{array} \right\},$$

similar equations for the 2nd population ($X_2(t)$, $Y_2(t)$).

- Can be extended to higher order delays in Erlang memory kernels \implies longer cascades of SDE's.
- We have the control on the weak error

$$\|P_t \varphi - \tilde{P}_t \varphi\|_\infty \leq Ct \frac{\|\varphi\|_{4,\infty}}{N^2}.$$

General comments

- We obtain a diffusion of high dimension driven by only 2 Brownian motions - each of them approximating the jump noise of one of the populations.
- We have to treat the **memory terms as auxiliary variables**. This gives rise to coordinates of the diffusion without noise \Rightarrow Highly degenerate diffusion.
- **Cascade structure** of the drift : a coordinate does only depend on itself and the following coordinate.

- Due to the **cascade structure** of the drift it is easy to show that the diffusion satisfies the **weak Hörmander condition**.
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- Using a convenient **Lyapunov-function and the control theorem**
 $\implies \exists$ attainable point (which can be chosen to be the unstable equilibrium of the limit monotone cyclic feedback system).
 \implies diffusion is **recurrent in the sense of Harris**, with unique invariant probability measure.

Theorem

Let Γ be a non constant periodic orbit of the limit system which is asymptotically orbitally stable. Then for all $\varepsilon > 0$ and for all $T > 0$, for all starting configurations x , P_x -almost surely,

the approx diffusion visits $B_\varepsilon(\Gamma)$ during a time period of length T , infinitely often.

Hence the diffusion approximation visits the oscillatory region infinitely often.

Large deviations

- **Large deviations result** : For large N , the diffusion stays within tubes around the limit cycle during long periods, before eventually leaving such a tube after a time which is of order

$$e^{N\bar{V}},$$

\bar{V} : quasi-potential, related to control problem : **cost of steering the process from the limit cycle to the boundary of the tube around the limit cycle.**

Large deviations

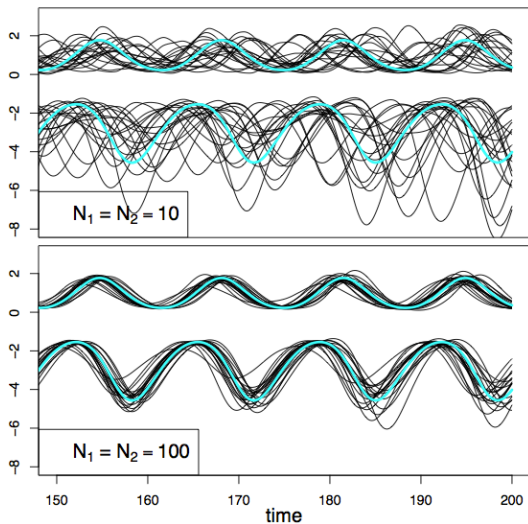
- **Large deviations result** : For large N , the diffusion stays within tubes around the limit cycle during long periods, before eventually leaving such a tube after a time which is of order

$$e^{N\bar{V}},$$

\bar{V} : quasi-potential, related to control problem : **cost of steering the process from the limit cycle to the boundary of the tube around the limit cycle.**

- Can be made precise in the sense of sample path large deviations for diffusions with small noise, in the sense of Freidlin-Wentzell (*although diffusion is highly degenerate*). Most important point : establish the **necessary control theory** in our framework. See Löcherbach JTP 2017 for details.

Some simulations of the approximating diffusion in the case $n = 2$



Conclusions

- Infinite memory (of Hawkes processes) and introduction of successive memory terms as auxiliary variables give rise to **hypo-elliptic diffusion approximation and its specific cascade structure**.
- This cascade structure implies :
 - weak Hörmander condition
 - controllability of the system
- Oscillations appear from the **non-linear “McKean-Vlasov”-type structure of the limit system** (system whose dynamics depends on its own law) - the dynamics of each single particle do not include any periodic behavior.

Remarks

- Specific interaction graph structure not necessary for propagation of chaos : other interaction graphs possible.
- What happens if there are **periodic changes in the underlying interaction graph** ?
- Example of a dynamical system where there are several coexisting stable orbits ?
- What happens when the **synaptic strength** (i.e. the factor c_k) changes over time (\rightarrow **plasticity** ?)
- And if we add an **external signal** during some time ?

Final remarks on Hawkes processes

- Erlang kernels allow to describe certain **Hawkes processes** via an associated system of **PDMP's**
- Their stability behavior can be easily analyzed.
- Gives another approach to **Simulation and Stability of non-linear Hawkes processes** (work with A. Duarte and G. Ost, 2017).

Some literature

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