



A Lagrangian model of Copepod dynamics in turbulent flows

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**Laboratoire
Mécanique
Lille**



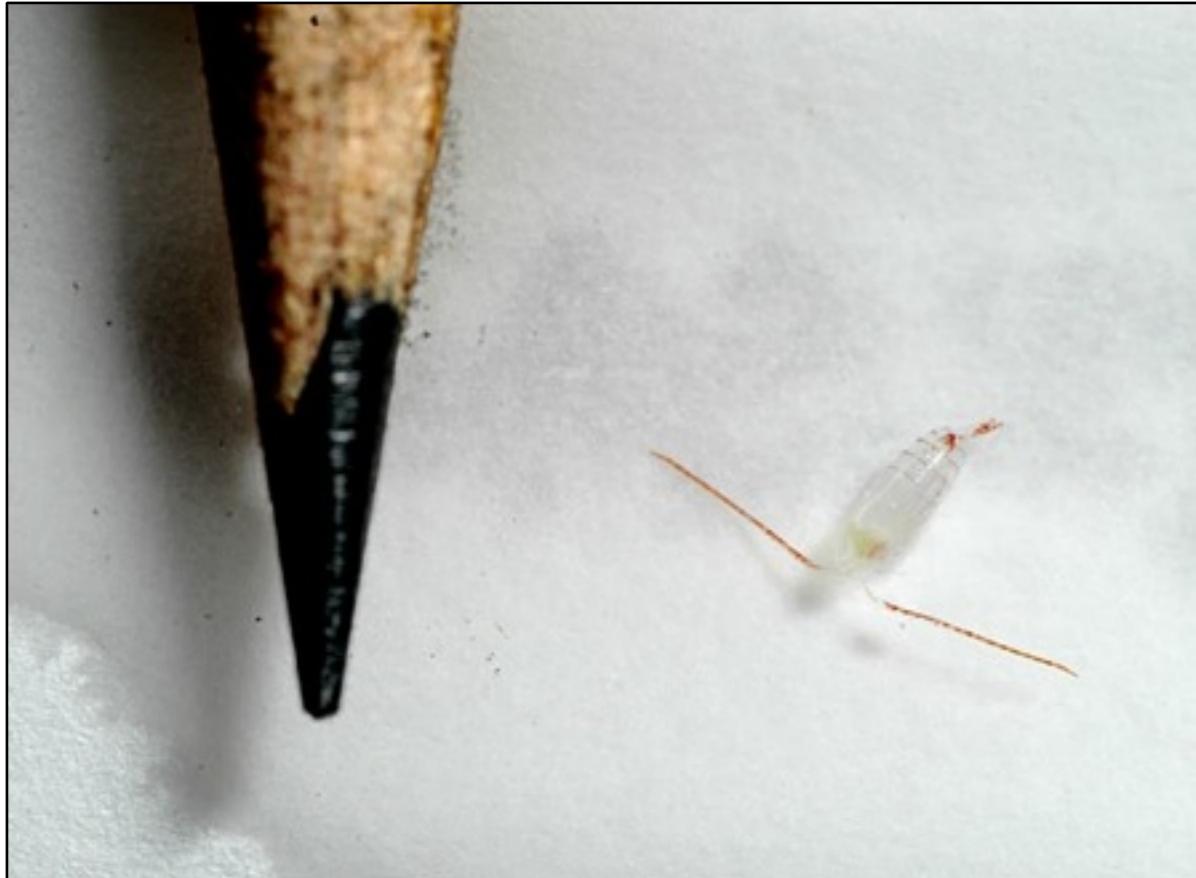
Lorentz Center, Leiden february 8th, 2016



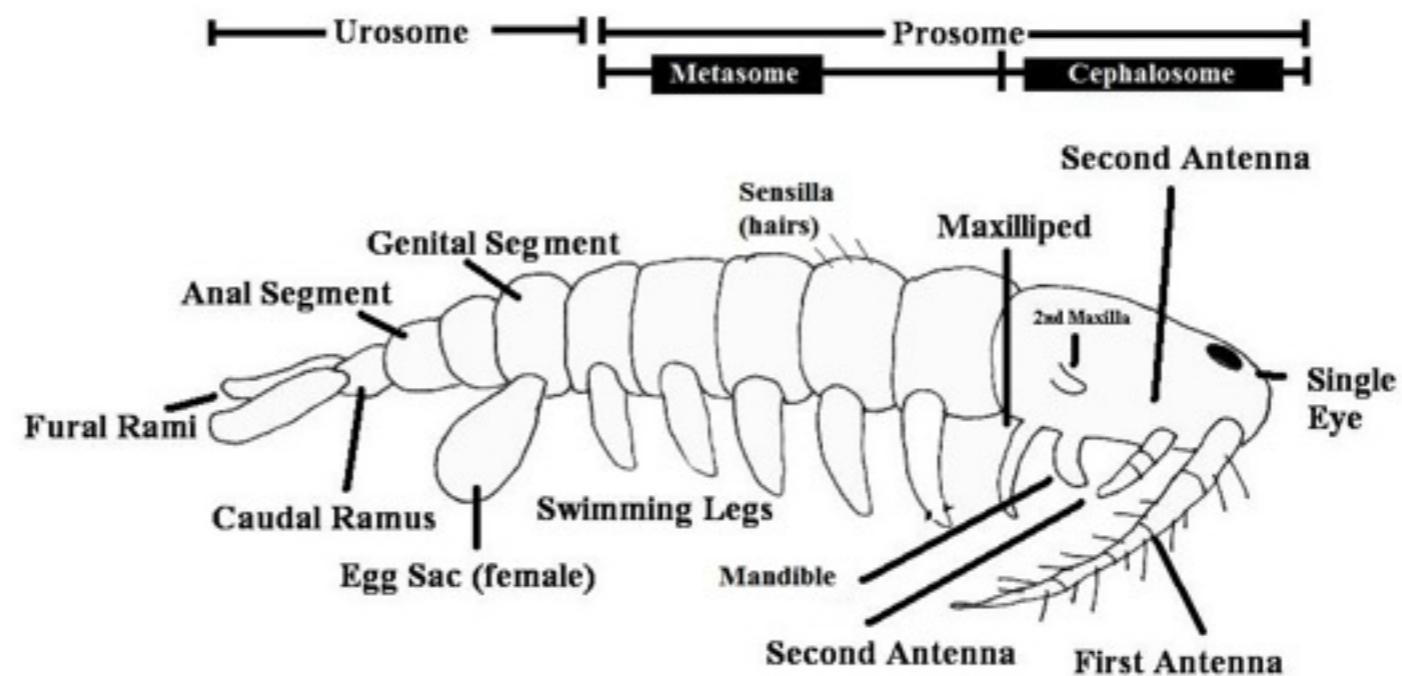
Outline

- Single Copepod dynamics (the essential)
- Results from a Simple Experiment
- A Lagrangian Copepod Model
- Numerical experiment with Turbulence
- Analysis and Main lessons
- Perspectives

Copepods size and shape



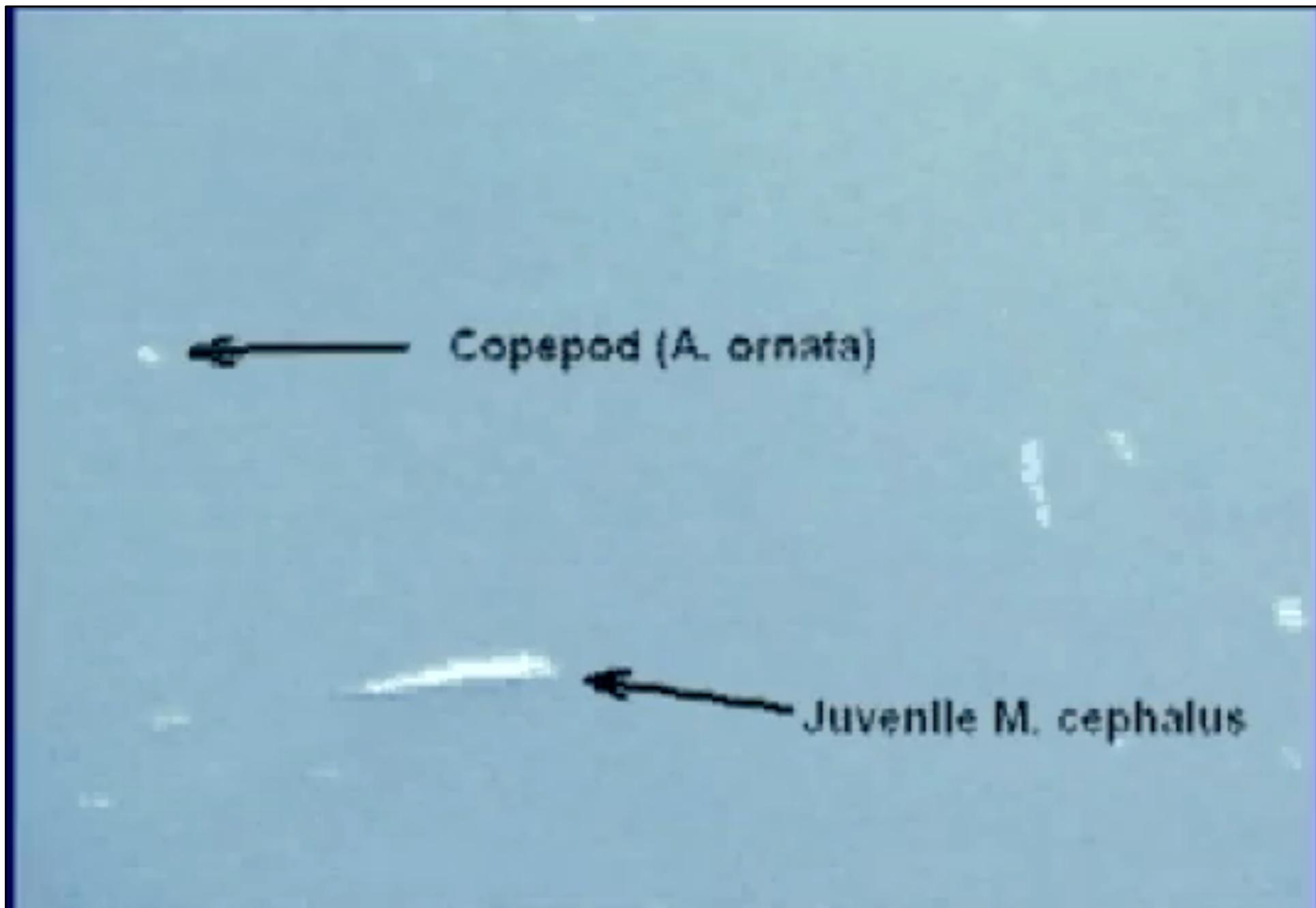
- Group of crustaceans
- 9000 species
- **size 0.5mm to 15 mm**
- aspect ratio 3-5





Copepods locomotion

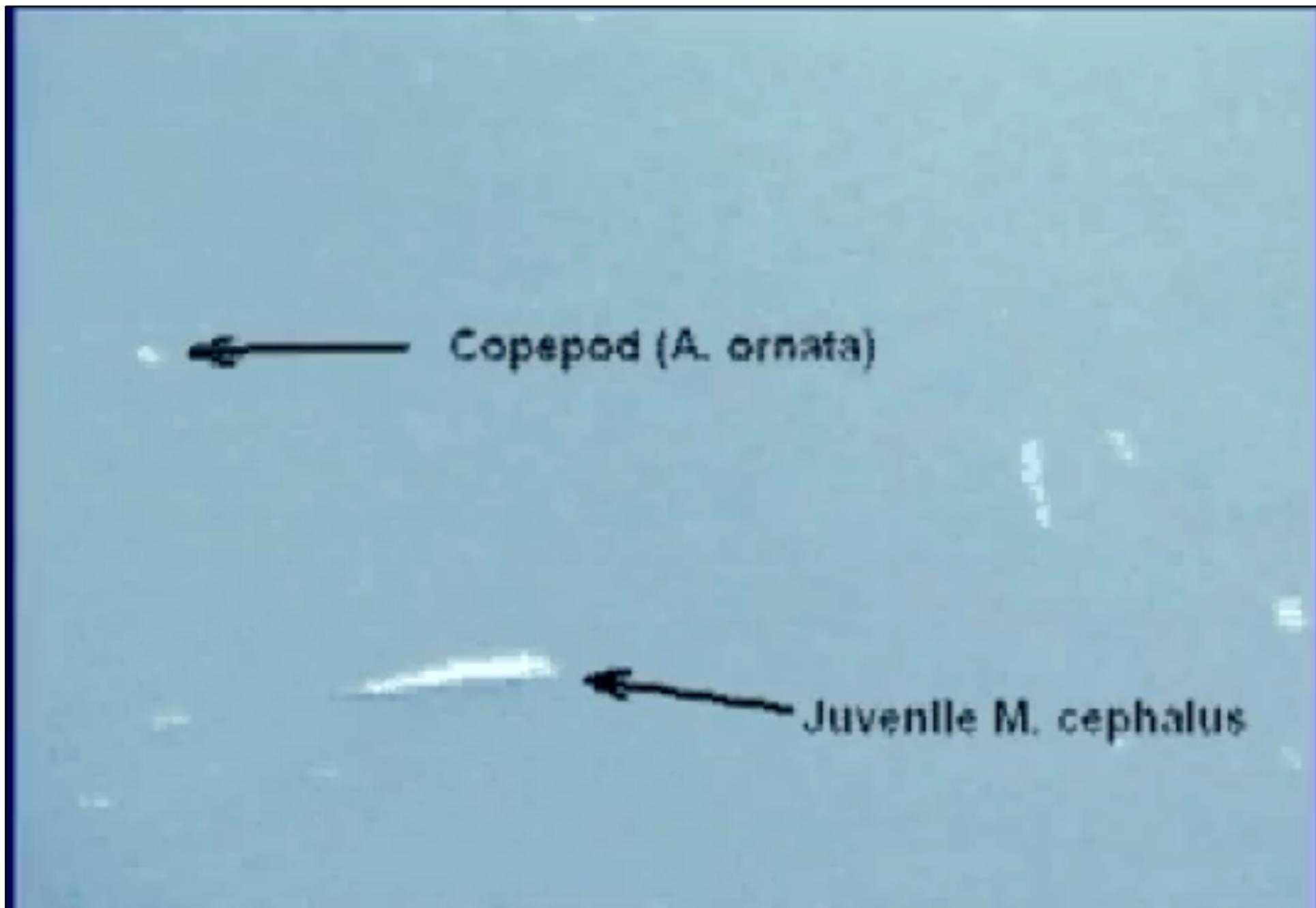
Main feature: Swimming by jumps





Copepods locomotion

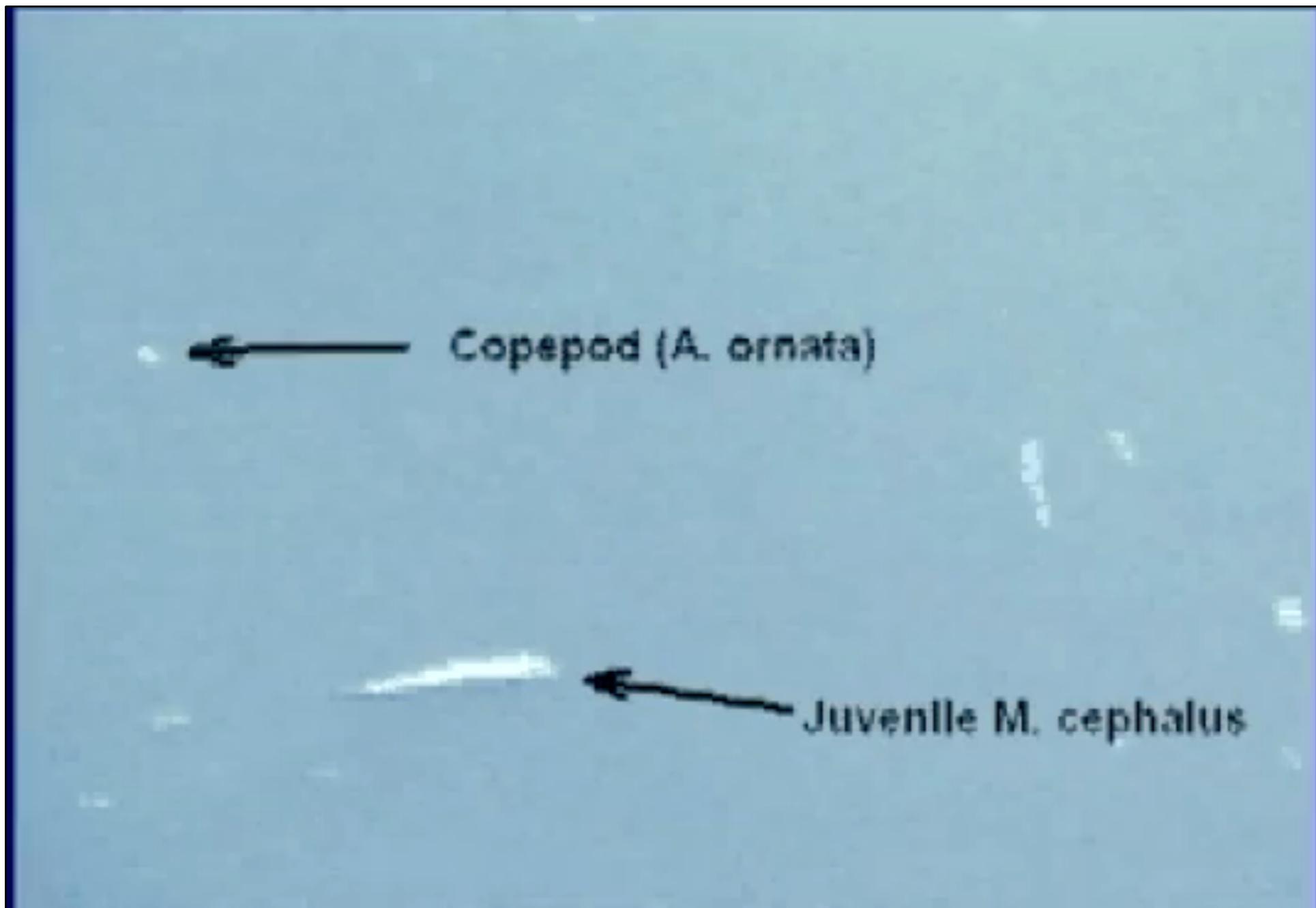
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Copepods locomotion

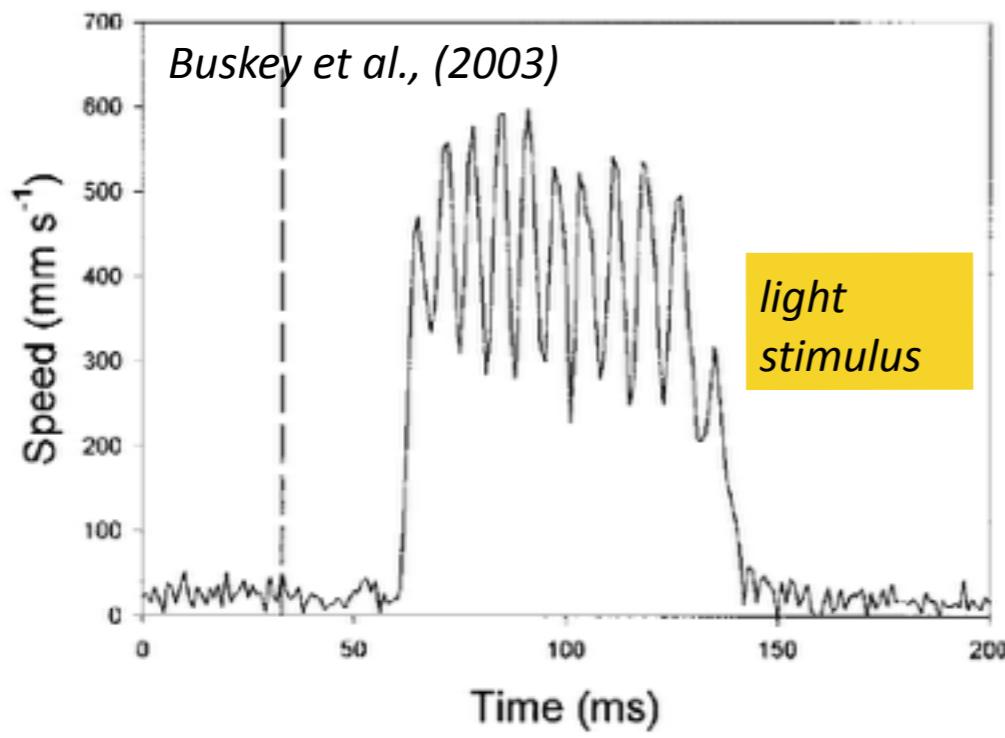
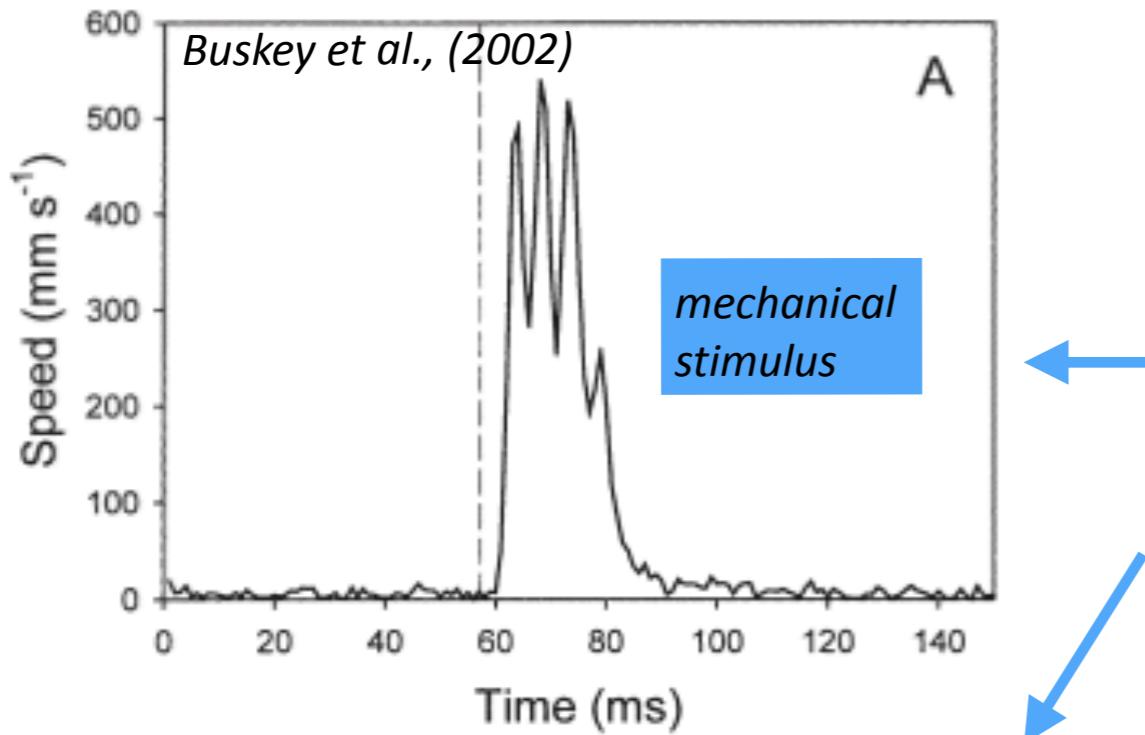
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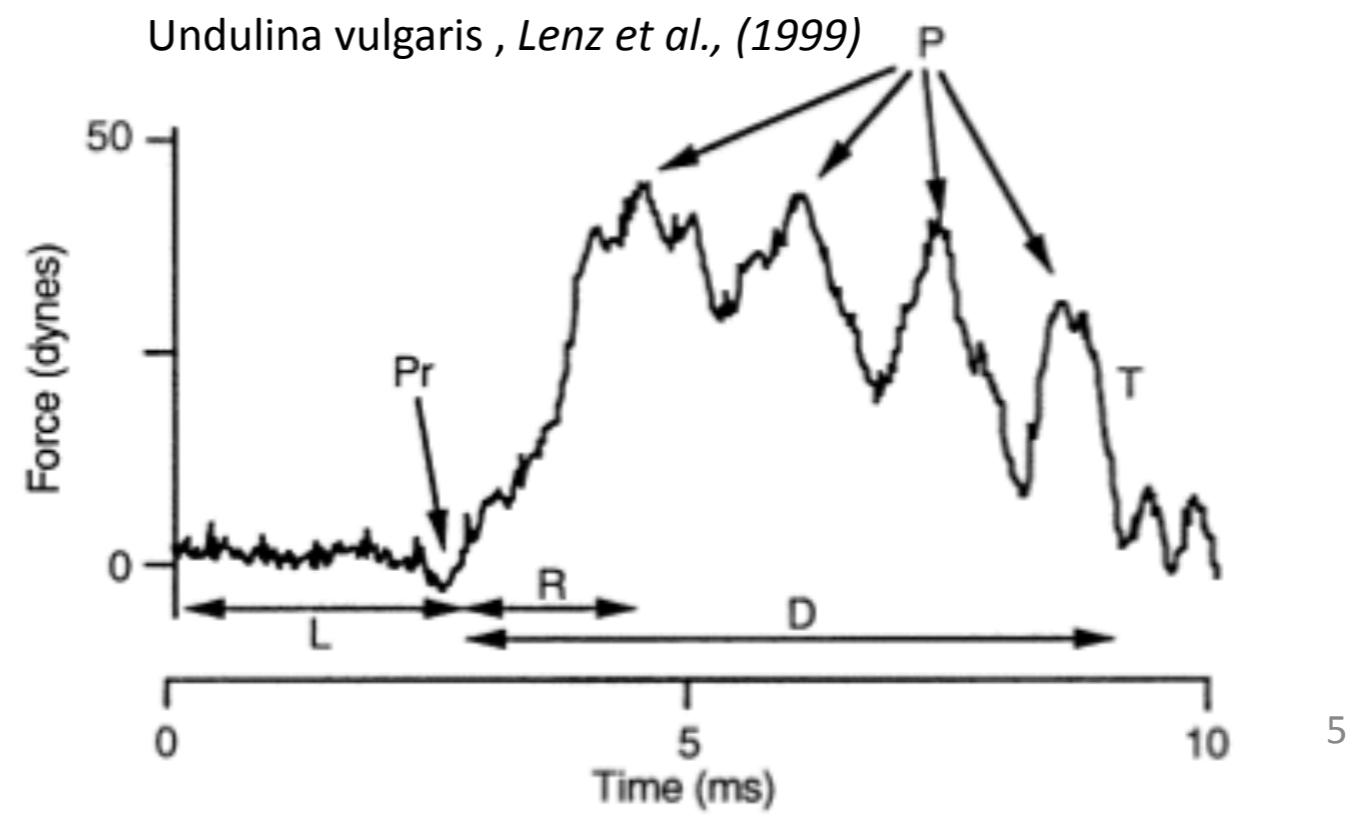
Copepods locomotion

Jump response to light and mechanical signals



Acartia tonsa:

- Stimulus (dashed line)
- Initiation of the escape response (3ms delay for mechanical)
- Acceleration during initial escape $\sim 10 \text{ g!}$

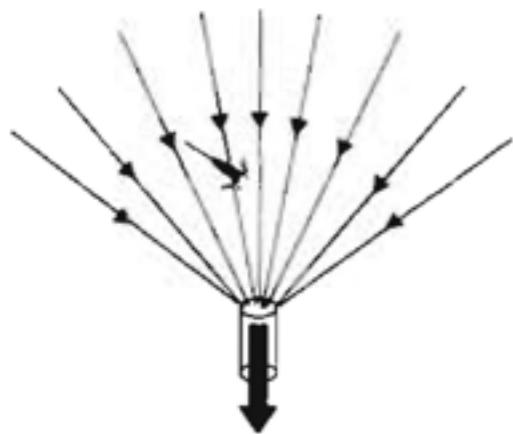




Copepods reaction to disturbances

Copepods react to deformation rate

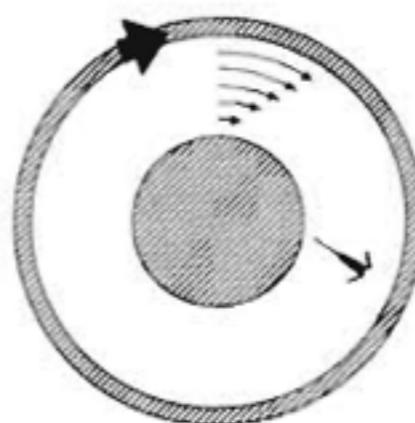
Kiørboe & Visser (1999)



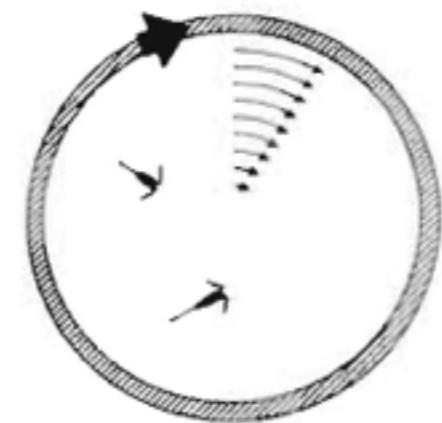
Siphon flow
• longitudinal deformation
• acceleration



Oscillating chamber
• acceleration



Couette device
• shear deformation
• acceleration
• vorticity



Rotating cylinder
• acceleration
• vorticity

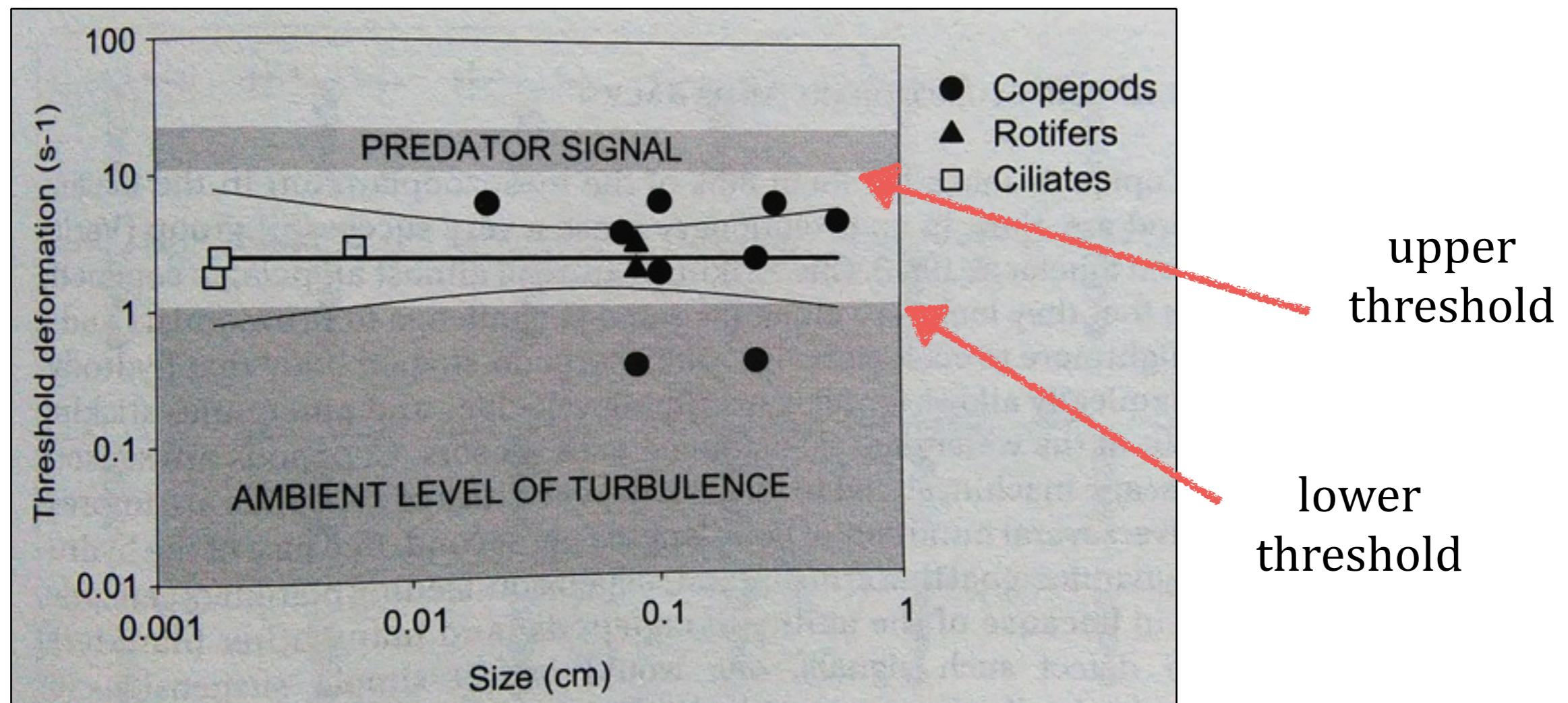
Acartia tonsa estimated threshold $\sim 0.4 \text{ s}^{-1}$

Threshold is copepod size dependent

Sensitivity to strain rate $\sim 0.025 \text{ s}^{-1}$ Woodson et al. (2005,2007)

Copepods reaction to disturbances

Copepods comfort region

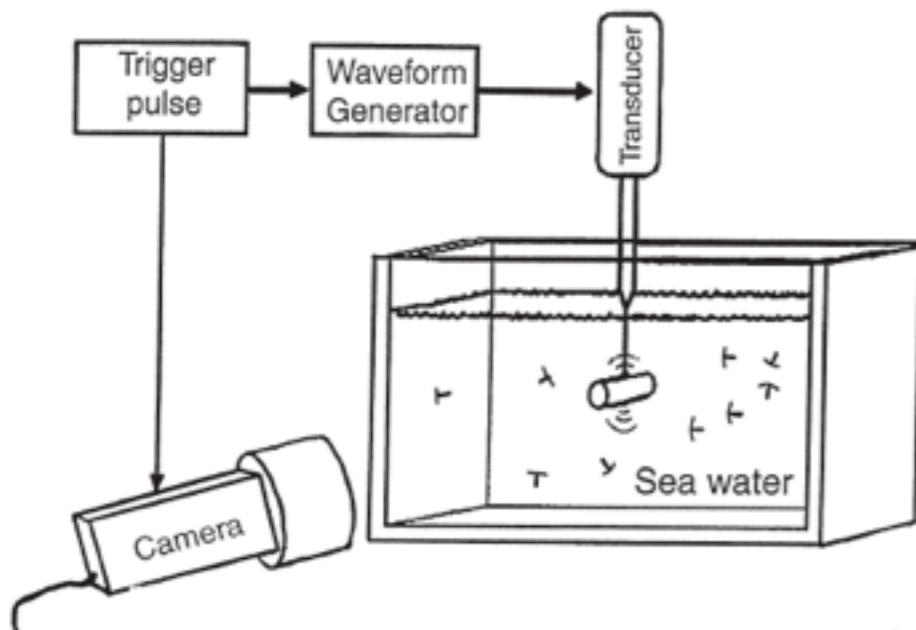


From T. Kiørboe, *A Mechanistic Approach to Plankton Ecology*, (2008)

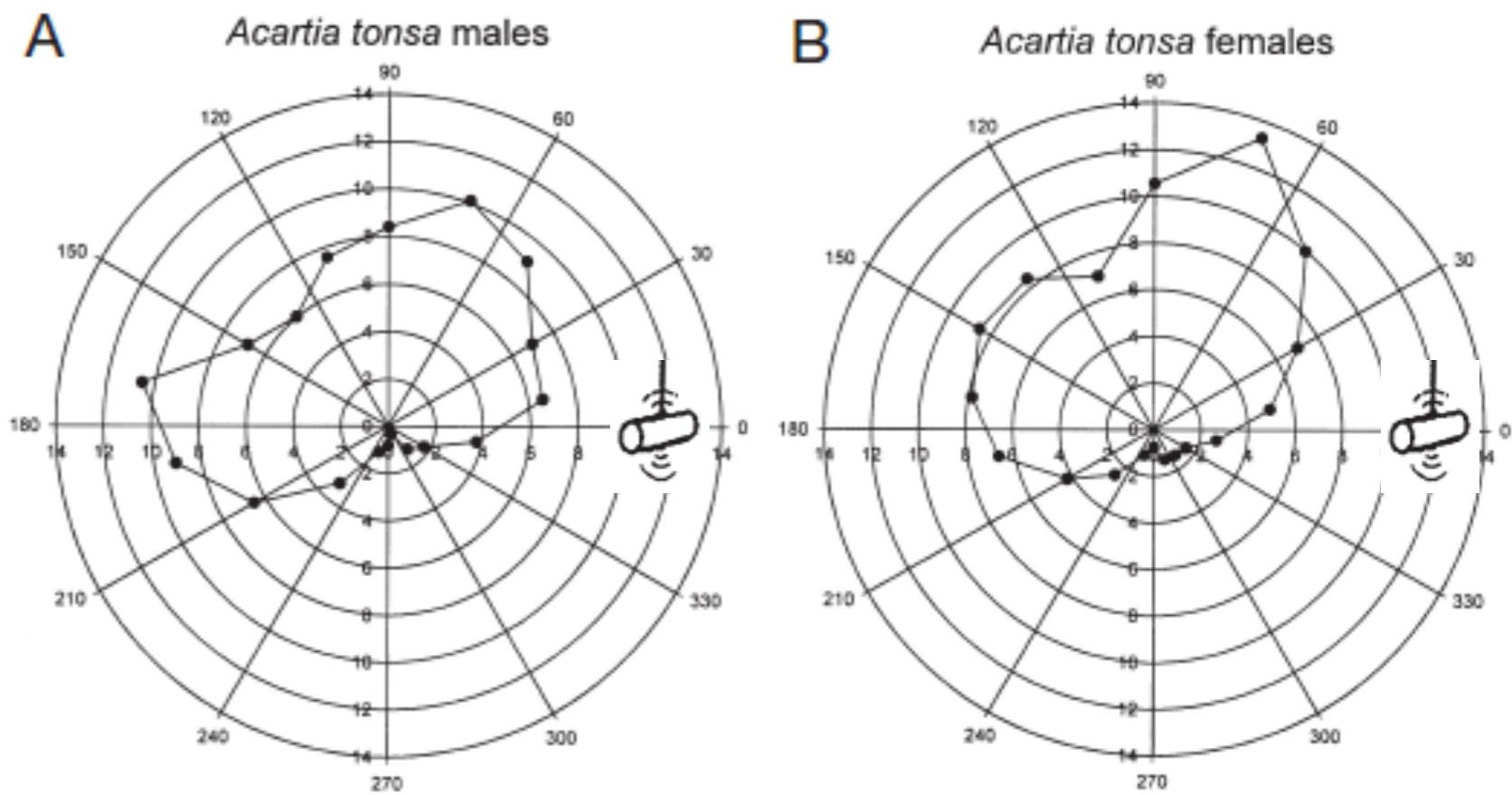


Copepods reaction to disturbances

Direction of Escape



Buskey et all., (2002)

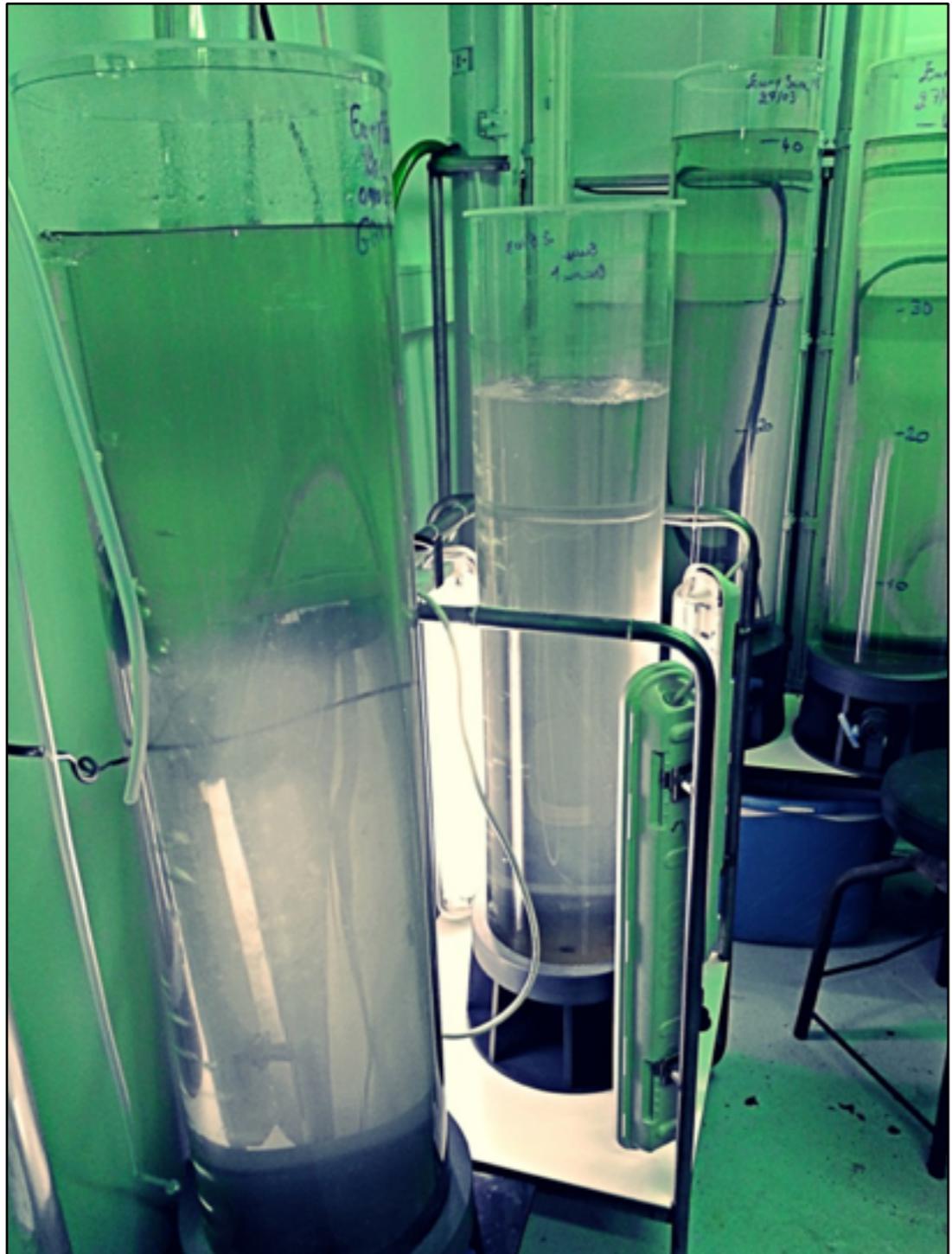


Escapes often begin with rapid reorientation away from the source of the disturbance, with maximum turning rates of about $30^\circ ms^{-1}$



Simple experiment

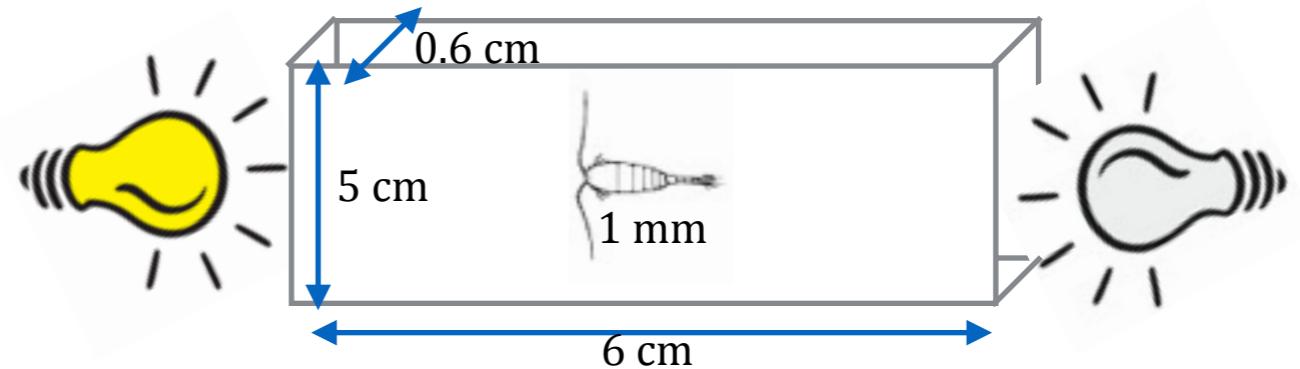
Copepods cultures at LOG Lab in Wimereux (France)



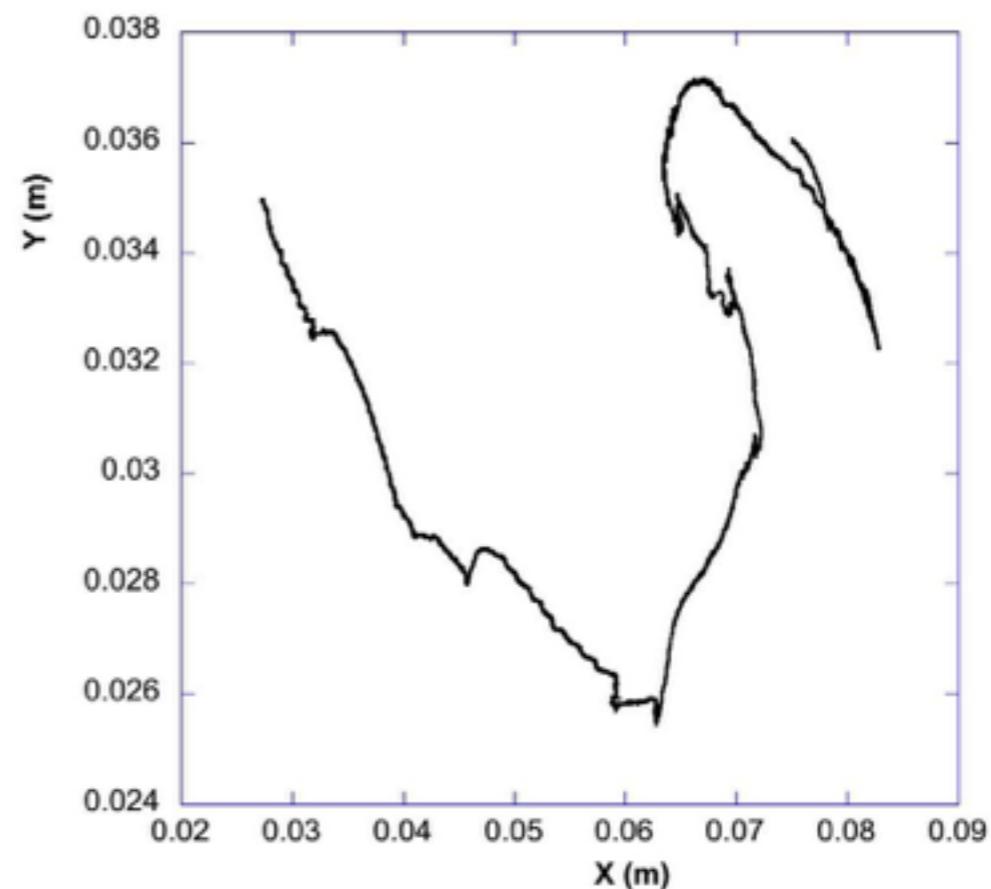


Simple experiment

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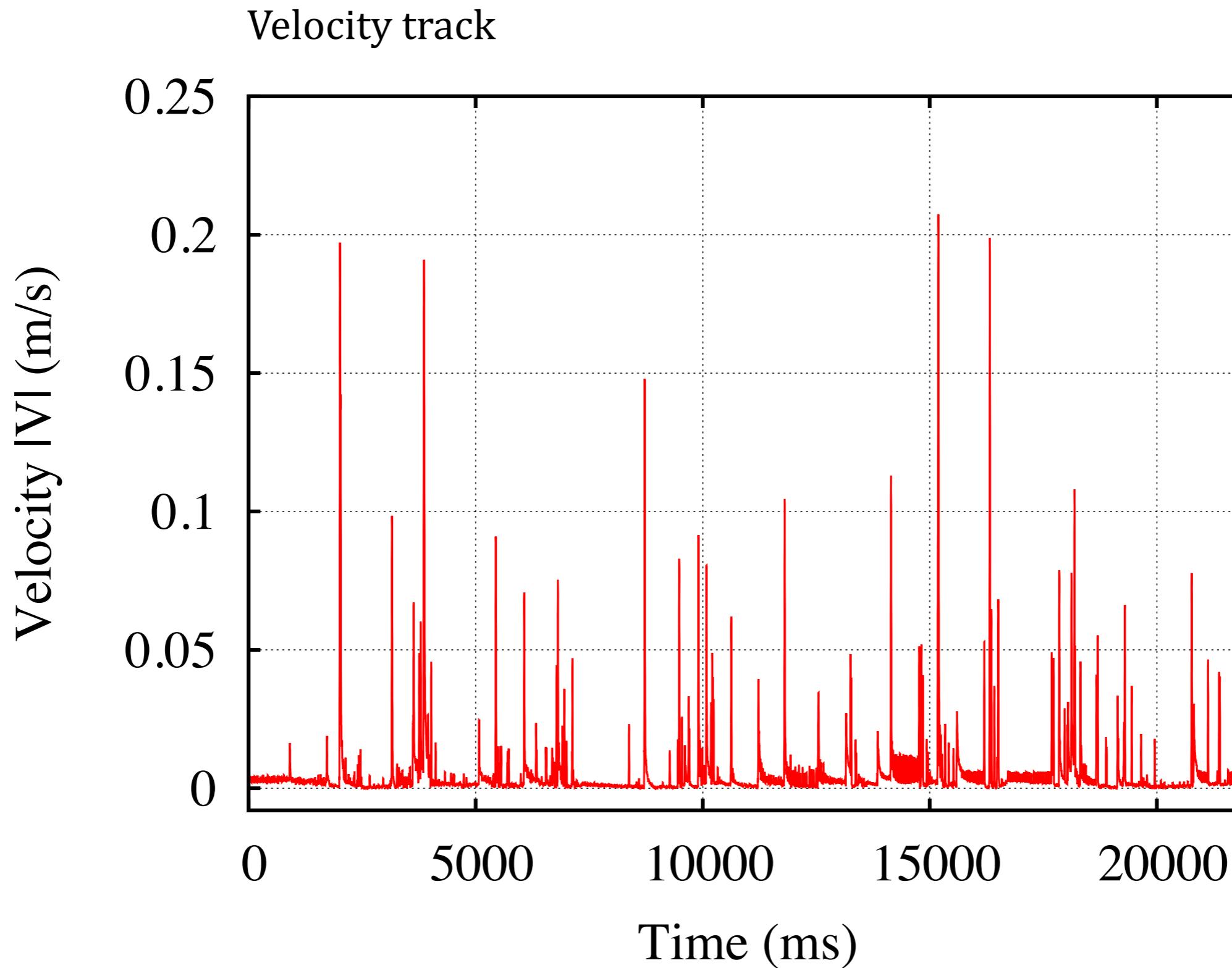


Response to **light stimuli**
of copepod "*Eurytemora affinis*"
in **still water**





Jump Data Analysis (1)





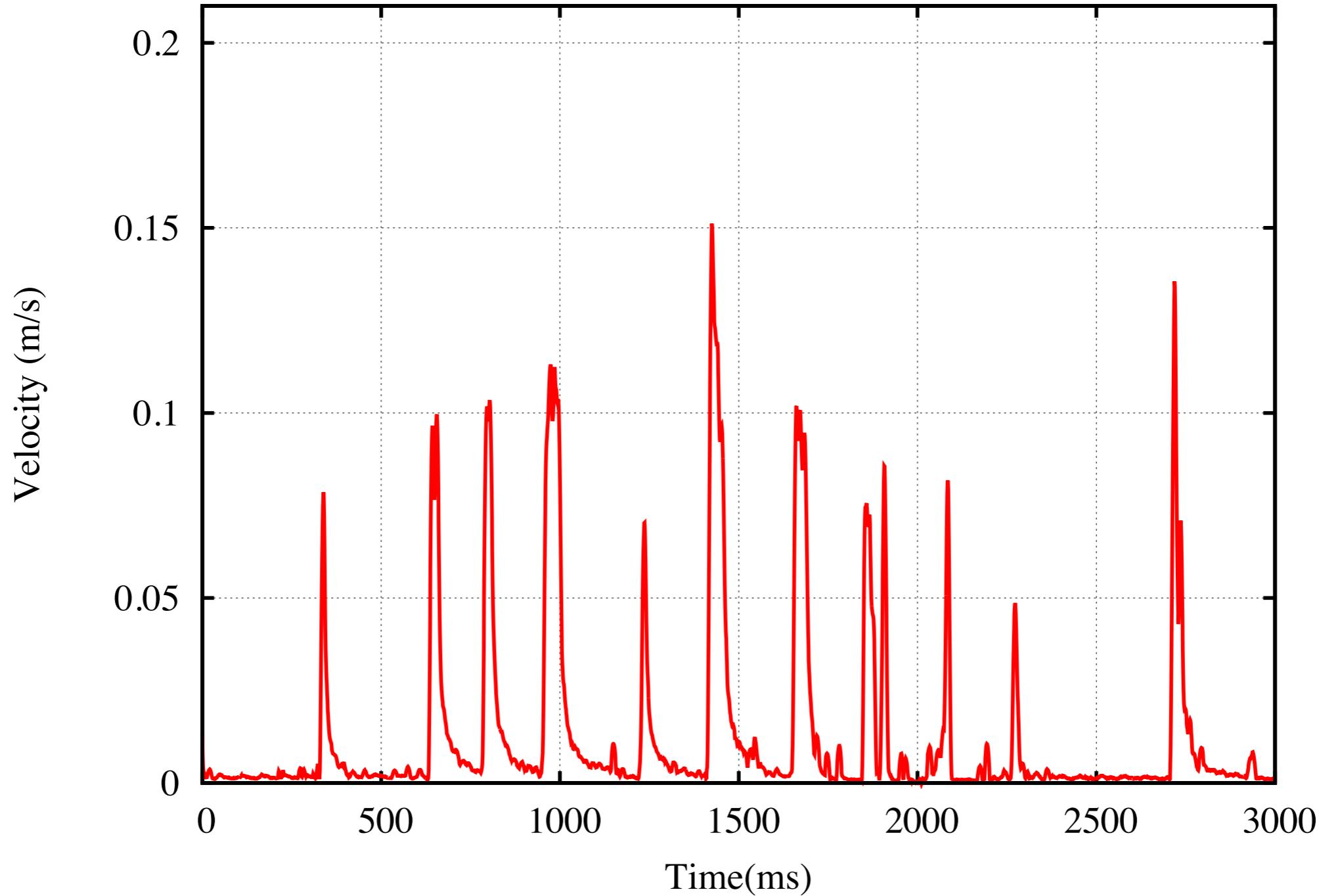
Jump Data Analysis (2)

Zooming in...



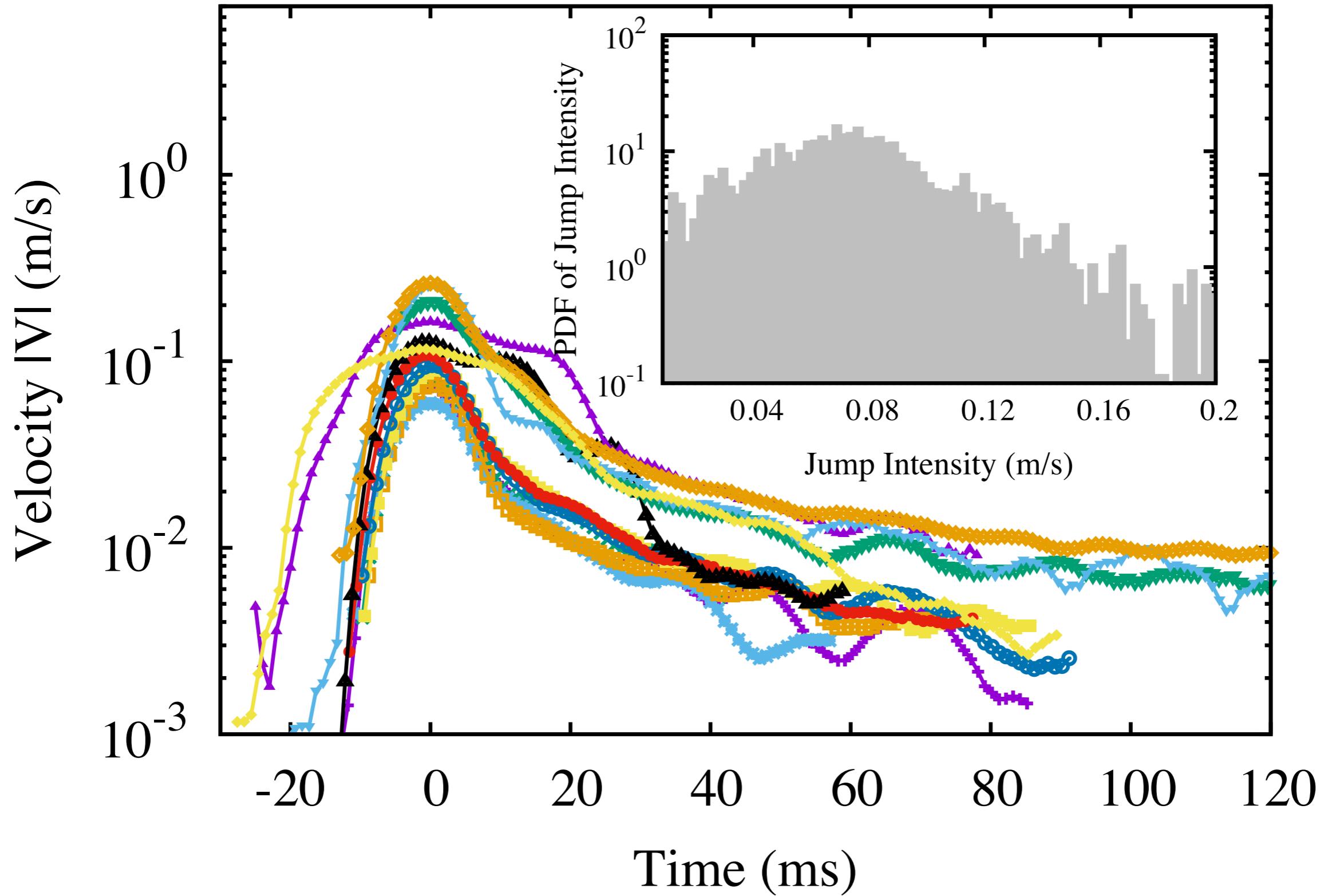
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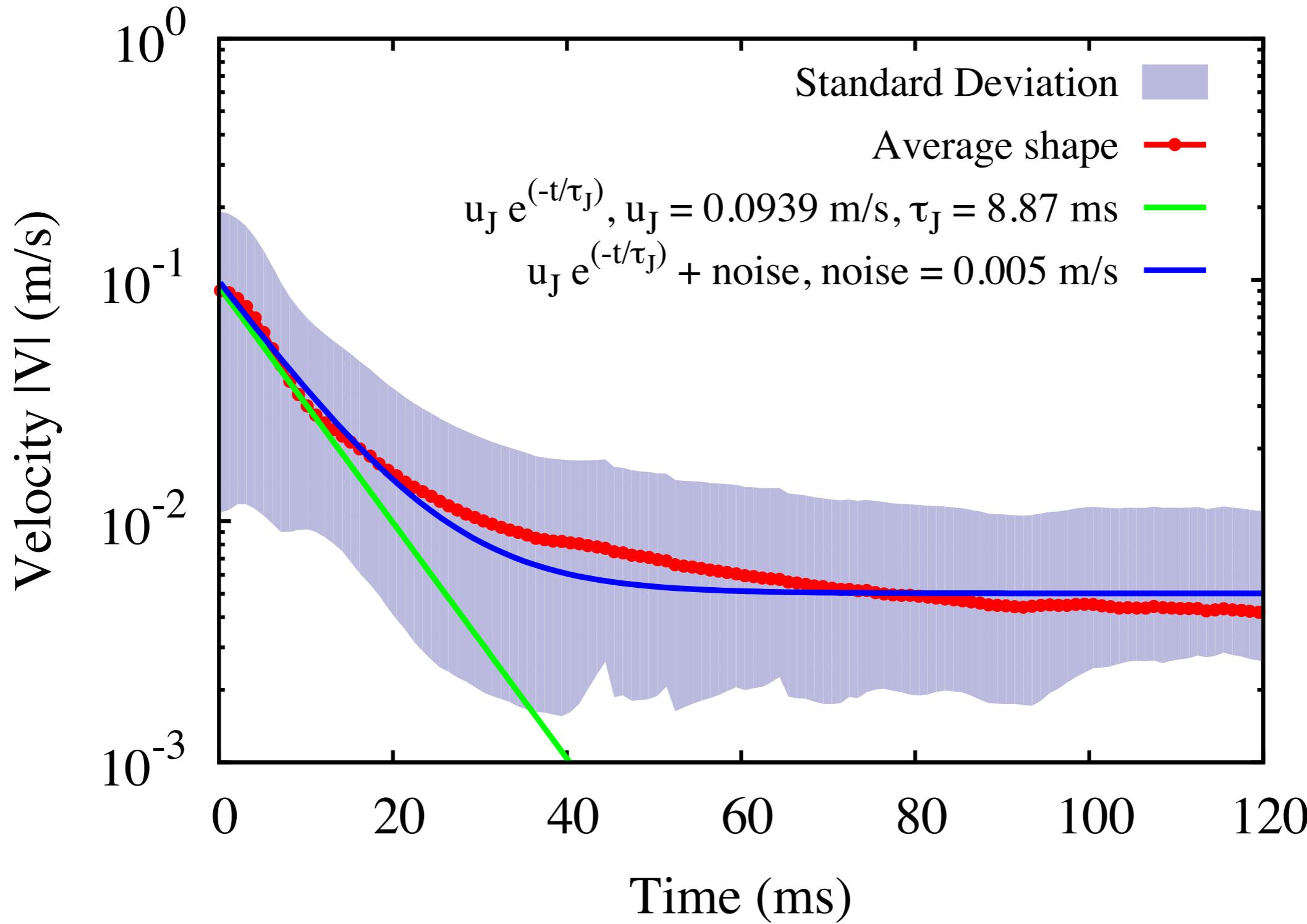


Jump Data Analysis (3)



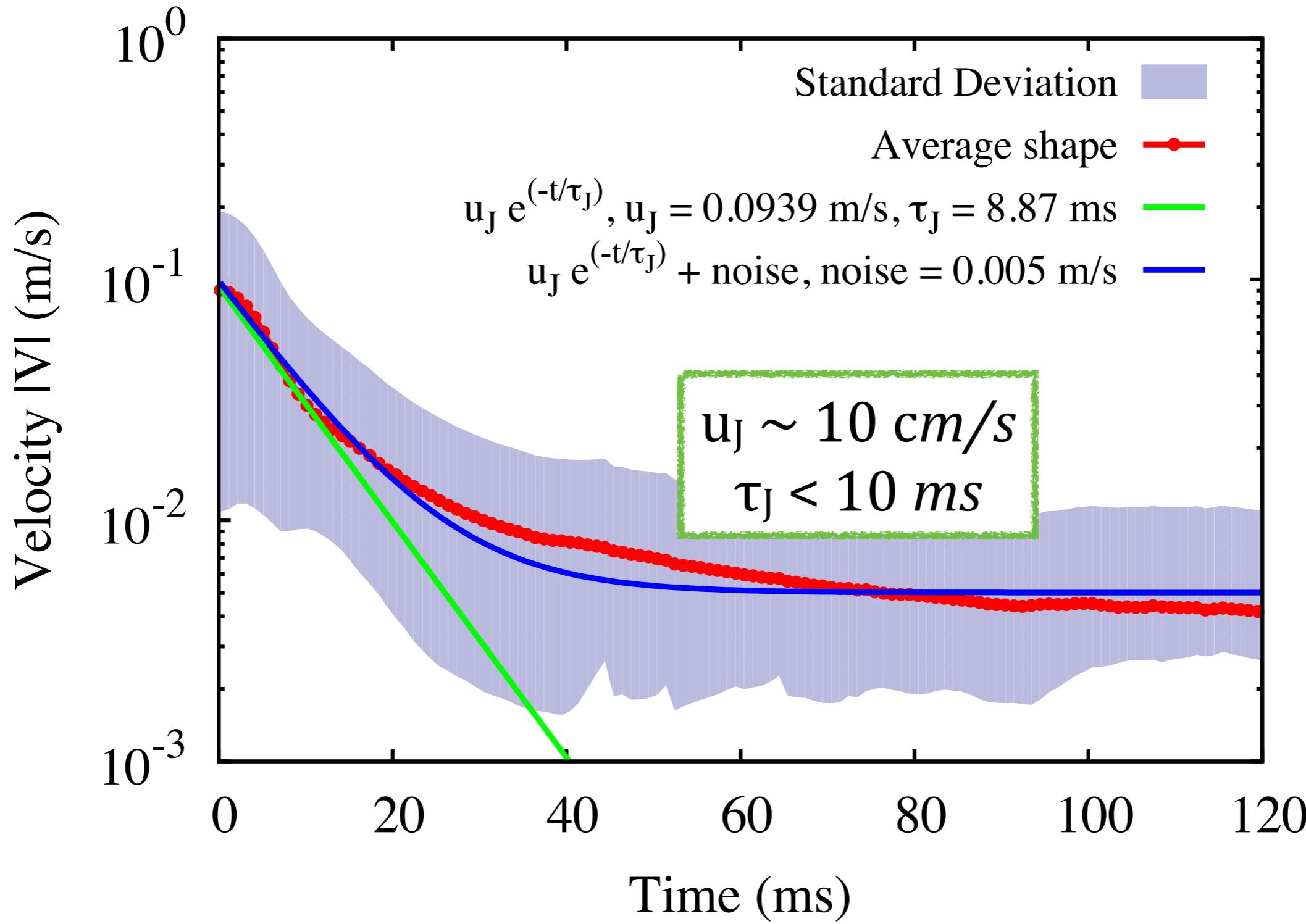


Jump Data Analysis (4)





Jump Data Analysis (4)





Hydrodynamical forces on a particle in a flow

Point-like model

$$\mathcal{V} \rho_p \ddot{\mathbf{X}} = \mathbf{F}_P + \mathbf{F}_{AM} + \mathbf{F}_D + \mathbf{F}_H + \mathbf{F}_L + \mathbf{F}_B + \mathbf{F}_{FX}$$

pressure
gradient

added
mass

Stokes
drag

History
drag

Lift

Buoyancy

Faxen

$$\mathbf{F}_P = \mathcal{V} \rho_f \frac{D\mathbf{U}}{D\tau}$$

$$\mathbf{F}_{AM} = \mathcal{V} \rho_f C_M \left(\frac{D\mathbf{U}}{D\tau} - \ddot{\mathbf{X}} \right)$$

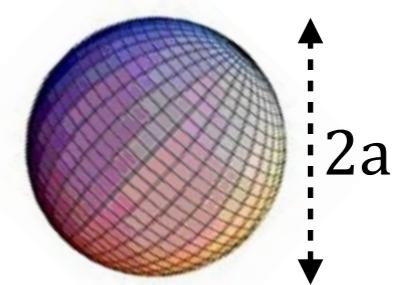
$$\mathbf{F}_D = 6 a \pi \mu (\mathbf{U} - \dot{\mathbf{X}})$$

$$\mathbf{F}_H = 6 a^2 \sqrt{\pi \nu} \int_0^\tau \frac{1}{\sqrt{\tau - \tau}} \frac{d(\mathbf{U} - \dot{\mathbf{X}})}{d\tau} d\tau$$

$$\mathbf{F}_L = \mathcal{V} \rho_f C_L (\mathbf{U} - \dot{\mathbf{X}}) \times \boldsymbol{\Omega}$$

$$\mathbf{F}_B = \mathcal{V} (\rho_p - \rho_f) g \hat{\mathbf{e}}_z$$

$$\mathbf{F}_{FX} : \left(\frac{D\mathbf{U}}{D\tau}, \mathbf{U} \right) \rightarrow \left(\langle \frac{D\mathbf{U}}{D\tau} \rangle_{\mathcal{V}}, \langle \mathbf{U} \rangle_{\mathcal{S}} \right)$$





Hydrodynamical forces on a particle in a flow (2)

Point-like model

$$\mathcal{V} \rho_p \ddot{\mathbf{X}} = \mathbf{F}_P + \mathbf{F}_{AM} + \mathbf{F}_D + \mathbf{F}_H + \mathbf{F}_L + \mathbf{F}_B + \mathbf{F}_{FX}$$

pressure
gradient

added
mass

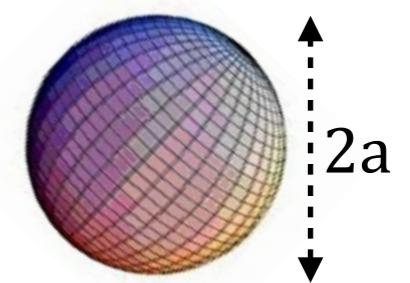
Stokes
drag

History
drag

Lift

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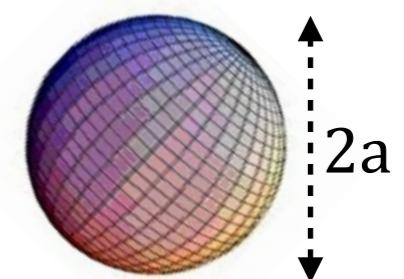


Hydrodynamical forces on a particle in a flow (2)

Major approximations

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pressure gradient added mass Stokes drag History drag Lift Buoyancy Faxen



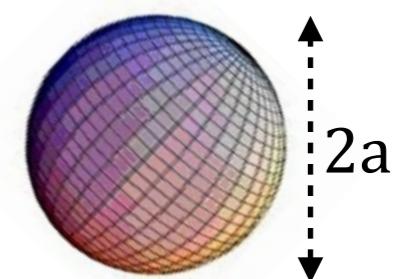
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pressure gradient added mass Stokes drag History drag Lift Buoyancy Faxen

$$\ddot{\mathbf{X}} = \frac{1}{\tau_p} (\mathbf{U} - \dot{\mathbf{X}})$$
$$\tau_p = \frac{2}{9} \frac{\rho_p}{\rho_f} \frac{a^2}{\nu}$$



Hydrodynamical forces on a particle in a flow (2)

Major approximations

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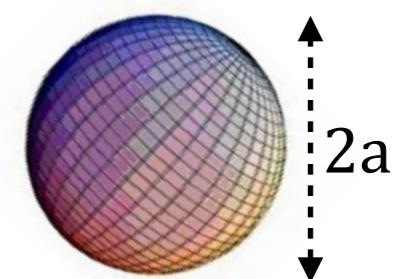
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formal solution

$$\dot{\mathbf{X}}(\mathcal{T}) = e^{-\mathcal{T}/\tau_p} \int_0^{\mathcal{T}} \frac{e^{t/\tau_p}}{\tau_p} \mathbf{U}(t) dt + \dot{\mathbf{X}}(0) e^{-\mathcal{T}/\tau_p}$$





Hydrodynamical forces on a particle in a flow (2)

Major approximations

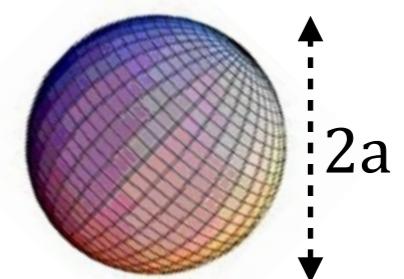
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Initial condition $\dot{\mathbf{X}}(0) = \mathbf{U}(0) + \mathbf{U}_J$

Slowly varying $\mathbf{U}(t)$

$$\dot{\mathbf{X}}(\mathcal{T}) \approx \mathbf{U}(0) + \mathbf{U}_J e^{-\mathcal{T}/\tau_p}$$

Hydrodynamical forces on a particle in a flow (2)

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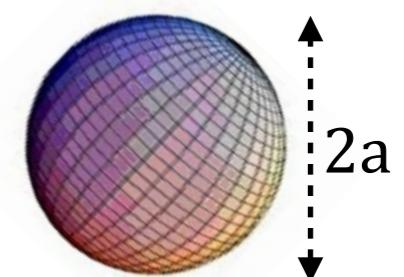
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Initial condition $\dot{\mathbf{X}}(0) = \mathbf{U}(0) + \mathbf{U}_J$

Slowly varying $\mathbf{U}(t)$

$$\dot{\mathbf{X}}(\mathcal{T}) \approx \mathbf{U}(0) + \mathbf{U}_J e^{-\mathcal{T}/\tau_p} \quad \longrightarrow$$

Our guess
 $\tau_p \sim \tau_J$



A minimal model

$$\dot{\mathbf{x}}(t) = \mathbf{u}(\mathbf{x}(t), t) + \mathbf{J}(t, t_i, t_e, \dot{\gamma}, \mathbf{p})$$

copepod
velocity

fluid
velocity

Jump
velocity term

Modified Chlamydomonas
Model



A minimal model

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copepod
velocity

fluid
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Jump
velocity term

Modified Chlamydomonas
Model

$$\mathbf{J}(t, t_i, t_e, \dot{\gamma}, \mathbf{p}) = H[\dot{\gamma}(t_i) - \dot{\gamma}_T] H[t_e - t] u_J e^{\frac{t_i - t}{\tau_J}} \mathbf{p}(t_i)$$

shear-rate
trigger

inhibition
time

exponential
decay

orientation

jump initial time

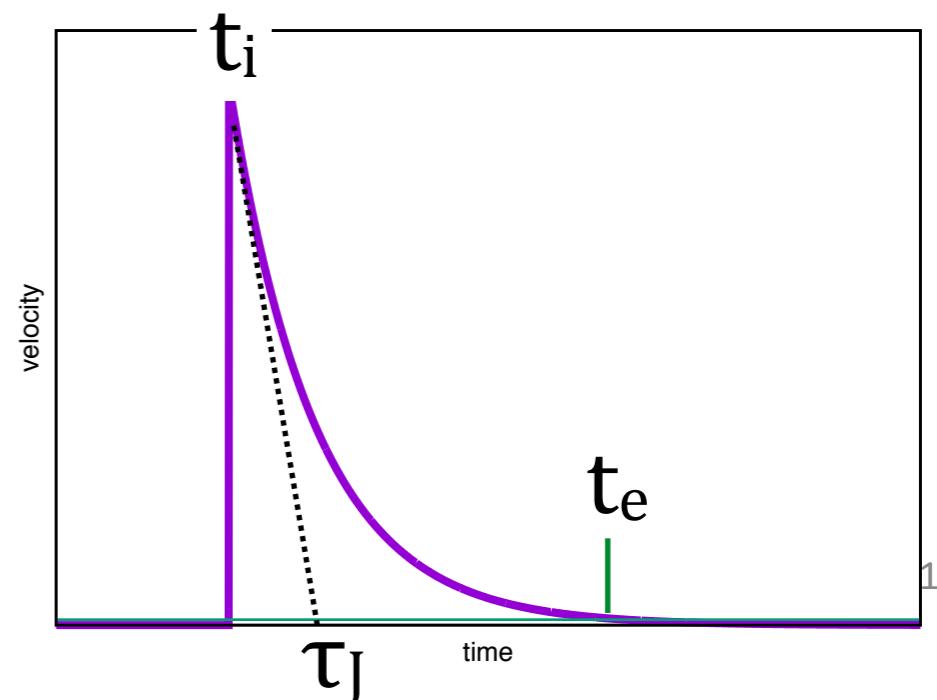
$$t_i = t \quad \text{if} \quad (\dot{\gamma}(t) > \dot{\gamma}_T) \cap (t > t_e)$$

jump end time

$$t_e = t_i + c \tau_J = t_i + \log(10^2) \tau_J$$

$\dot{\gamma}_T$ upper shear-rate
threshold value

$$\dot{\gamma} = \sqrt{2 \mathcal{S} : \mathcal{S}}$$



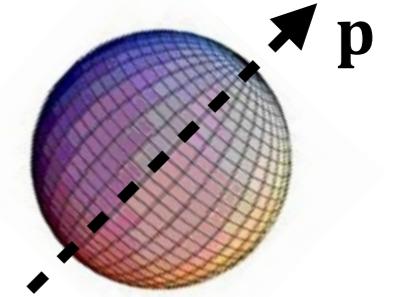
A minimal model (orientation)

Sphere

$$\dot{\mathbf{p}}(t) = \boldsymbol{\Omega} \cdot \mathbf{p}(t)$$

$$\Omega_{ij} = 1/2(\partial_i u_j - \partial_j u_i)$$

antisymmetric gradient tensor



Ellipsoid: Jeffery equation

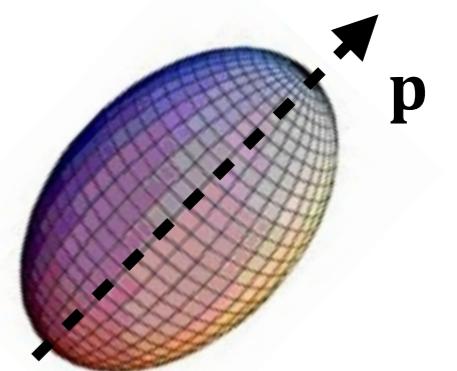
$$\dot{\mathbf{p}}(t) = \left(\boldsymbol{\Omega} + \frac{\alpha^2 - 1}{\alpha^2 + 1} (\mathcal{S} - \mathbf{p}^T(t) \cdot \mathcal{S} \cdot \mathbf{p}(t)) \right) \cdot \mathbf{p}(t)$$

$$S_{ij} = 1/2(\partial_i u_j + \partial_j u_i)$$

symmetric gradient tensor

$$\alpha \equiv l/d$$

Aspect ratio





A minimal model (summary)

Model assumptions:

- Rigid particle (spherical or ellipsoidal)
- neutral, homogeneous density
- Hydrodynamical forces: only Stokes Drag
- passive orientation
- Fixed response to external flow disturbances
- React to high shear-rate intensity (i.e. scalar single threshold)
- no-memory of previous jumps
- Model parameters: u_J τ_J , $\dot{\gamma}_T$, $(t_e - t_i)$



Lagrangian Copepods (LC) in a turbulent flow

In turbulent ocean flows:

Parameter	Unit	Range	
ν	$m^2 s^{-1}$	$\sim 10^{-6}$	
ϵ	$m^2 s^{-3}$	10^{-8}	10^{-4}
η	m	3×10^{-3}	3×10^{-4}
τ_η	s	10	0.1
u_η	ms^{-1}	3×10^{-4}	3×10^{-3}
Re_λ	—	$\mathcal{O}(10^2)$	



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$$u_J/u_\eta \sim O(10^2)$$

$$\tau_J/\tau_\eta \sim O(10^{-2})$$

$$\tau_\eta \dot{\gamma}_T \sim O(1)$$



Lagrangian Copepods (LC) in a turbulent flow

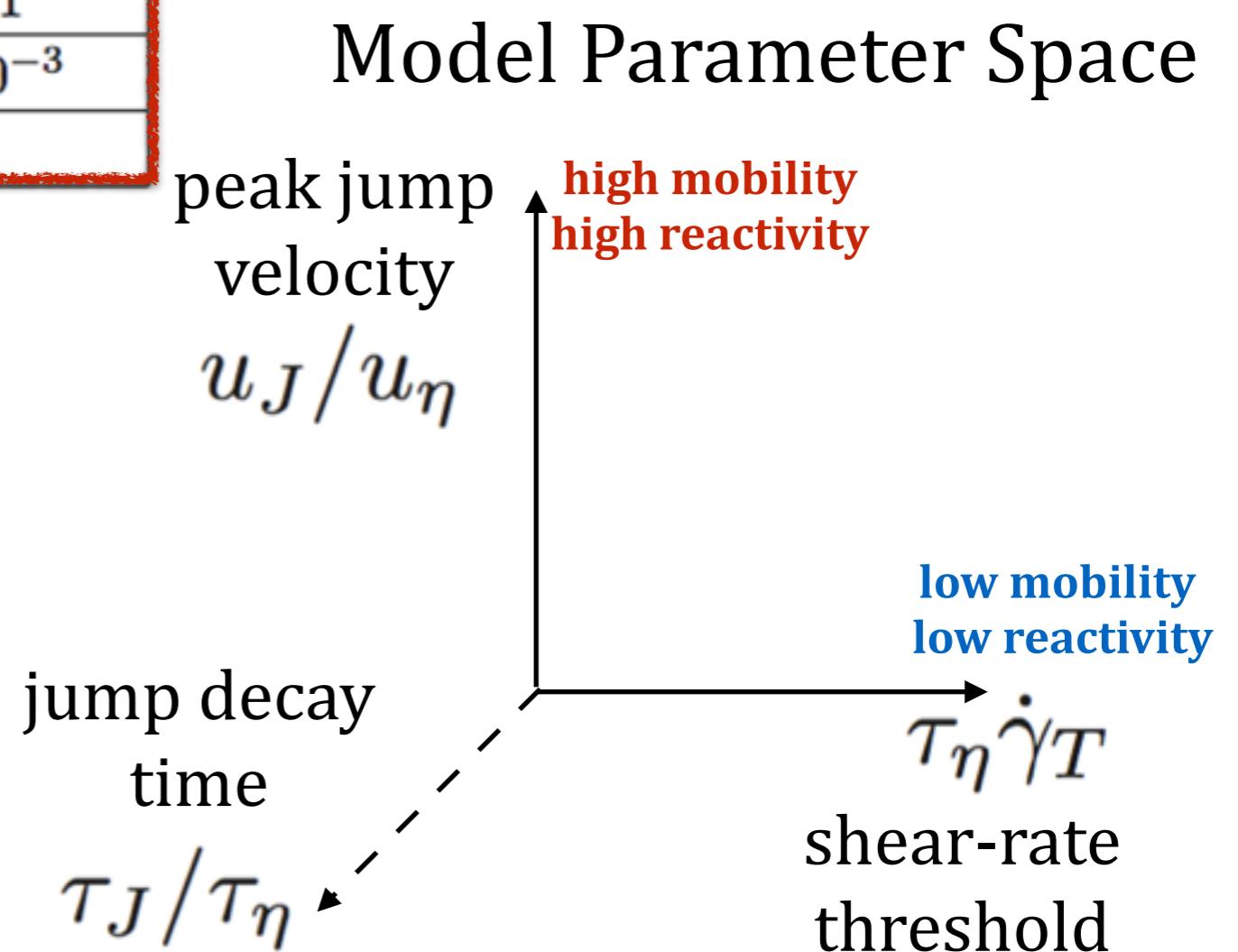
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Re_λ	-	$\mathcal{O}(10^2)$		

$$u_J/u_\eta \sim 0(10^2)$$

$$\tau_J/\tau_\eta \sim 0(10^{-2})$$

$$\tau_\eta \dot{\gamma}_T \sim 0(1)$$





Numerical Experiment

Lagrangian — Eulerian

LC model

$$\dot{\mathbf{x}}(t) = \mathbf{u}(\mathbf{x}(t), t) + \mathbf{J}(t, t_i, t_e, \dot{\gamma}, \mathbf{p})$$

Tracking of $\sim 10^6$ LC

families with different

$$u_J$$

$$\dot{\gamma}_T$$

$$\tau_J \sim 10^{-2} \tau_\eta$$

Homogeneous Isotropic Turbulence

$$\partial_t \mathbf{u} + \mathbf{u} \cdot \nabla \mathbf{u} = -\nabla p/\rho + \nu \Delta \mathbf{u} + \mathbf{f}$$

$$\nabla \cdot \mathbf{u} = 0$$

pseudo-spectral algorithm

$$Re_\lambda \sim 80$$

$$N = 128^3$$

3-periodic cube



Numerical Experiment

Lagrangian — Eulerian

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Will we
see clusters?



Numerical Experiment

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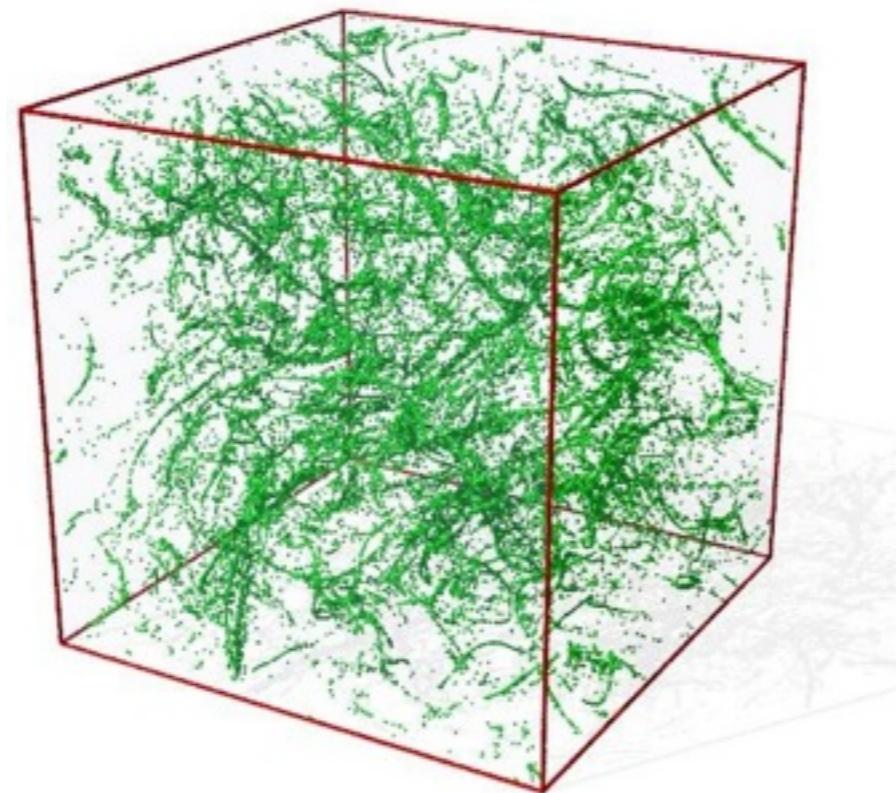
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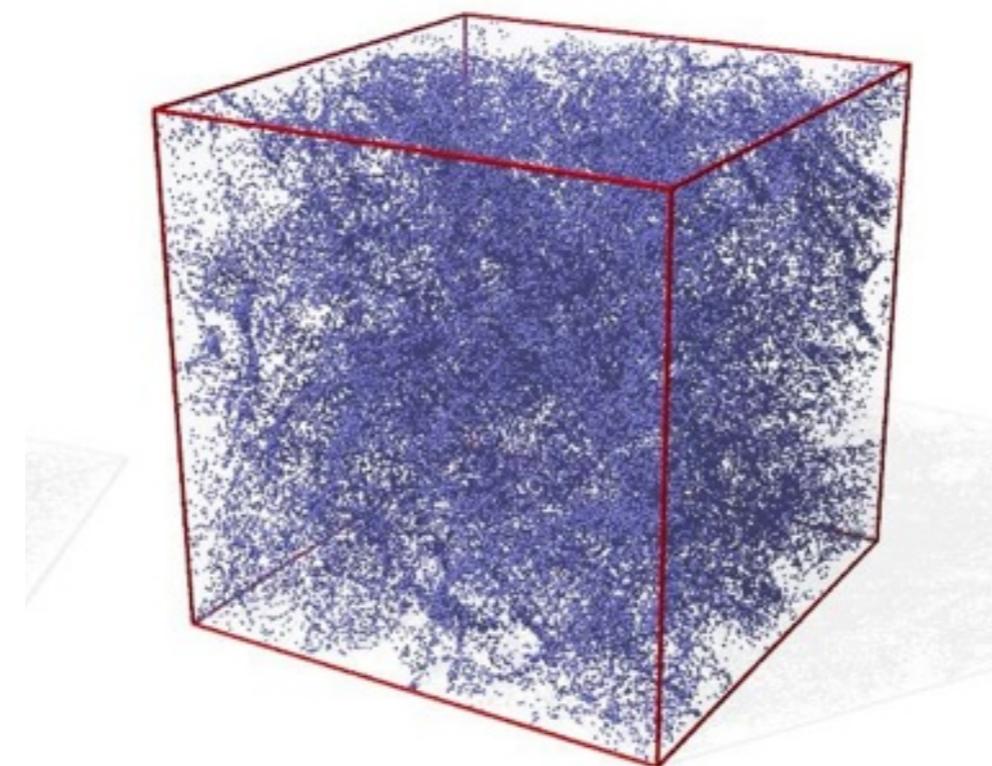
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$$\begin{aligned} u_J \\ \dot{\gamma}_T \\ \tau_J \sim 10^{-2} \tau_\eta \end{aligned}$$

Homogeneous Isotropic Turbulence

$$\partial_t \mathbf{u} + \mathbf{u} \cdot \nabla \mathbf{u} = -\nabla p/\rho + \nu \Delta \mathbf{u} + \mathbf{f}$$

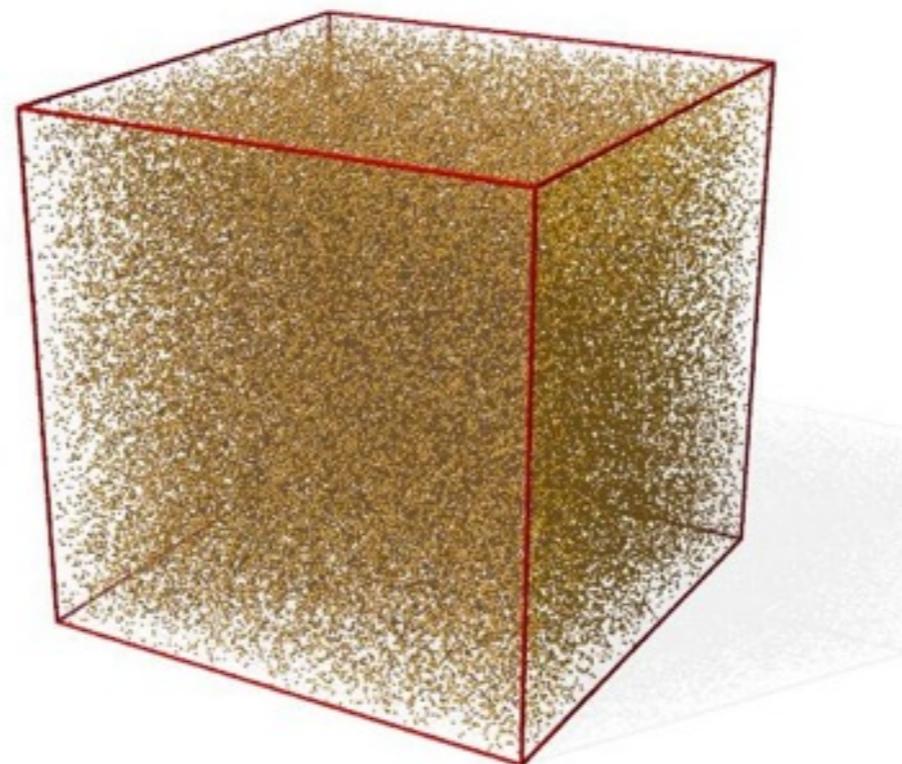
$$\nabla \cdot \mathbf{u} = 0$$

pseudo-spectral algorithm

$$Re_\lambda \sim 80$$

$$N = 128^3$$

3-periodic cube



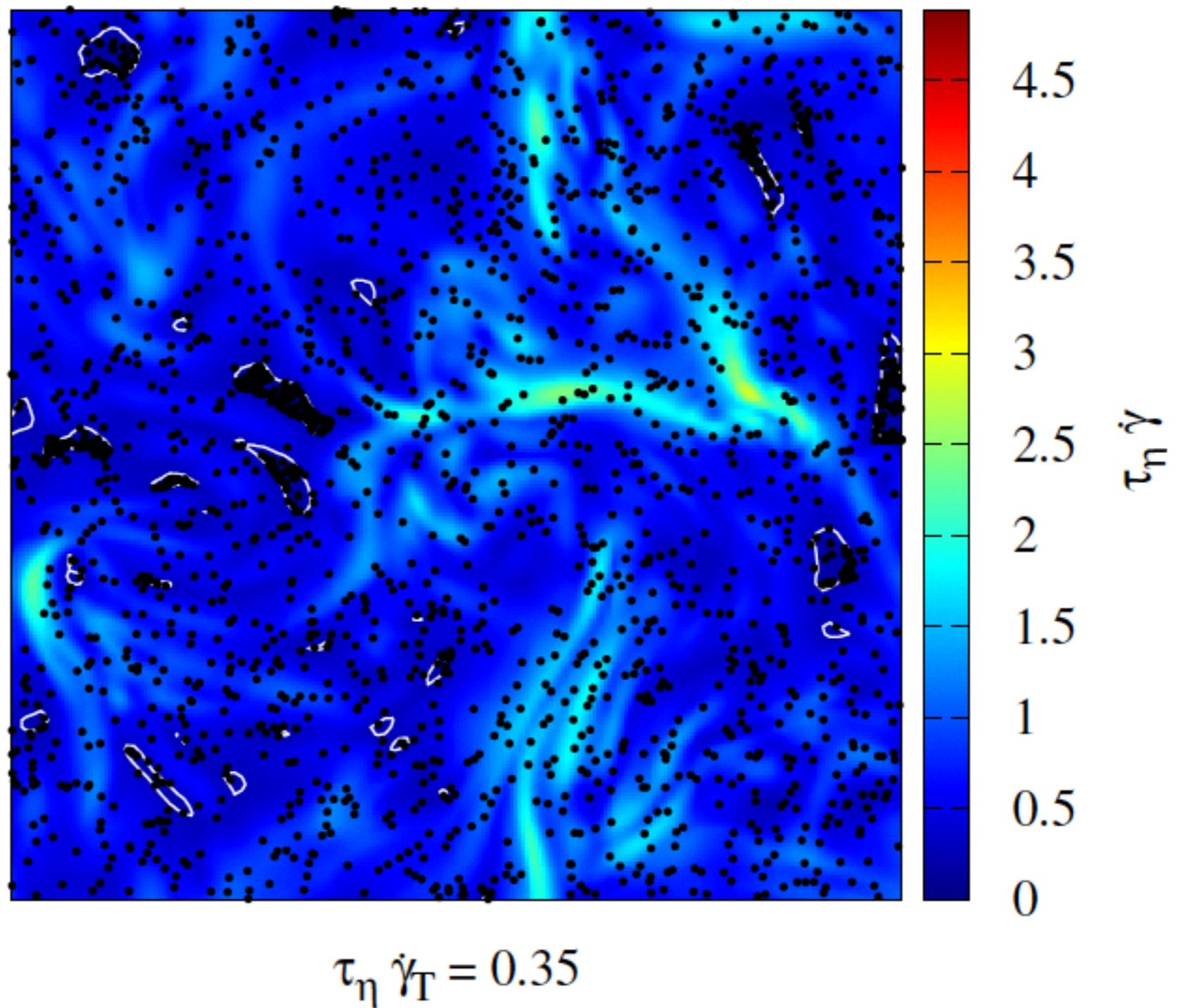


Spatial distribution

2D slice of thickness η , Jump intensity $u_J/u_\eta = 250$, $\tau_J = 10^{-2} \tau_\eta$

Jump shear-rate
threshold

1) Low, many  jumps, few
dense islands



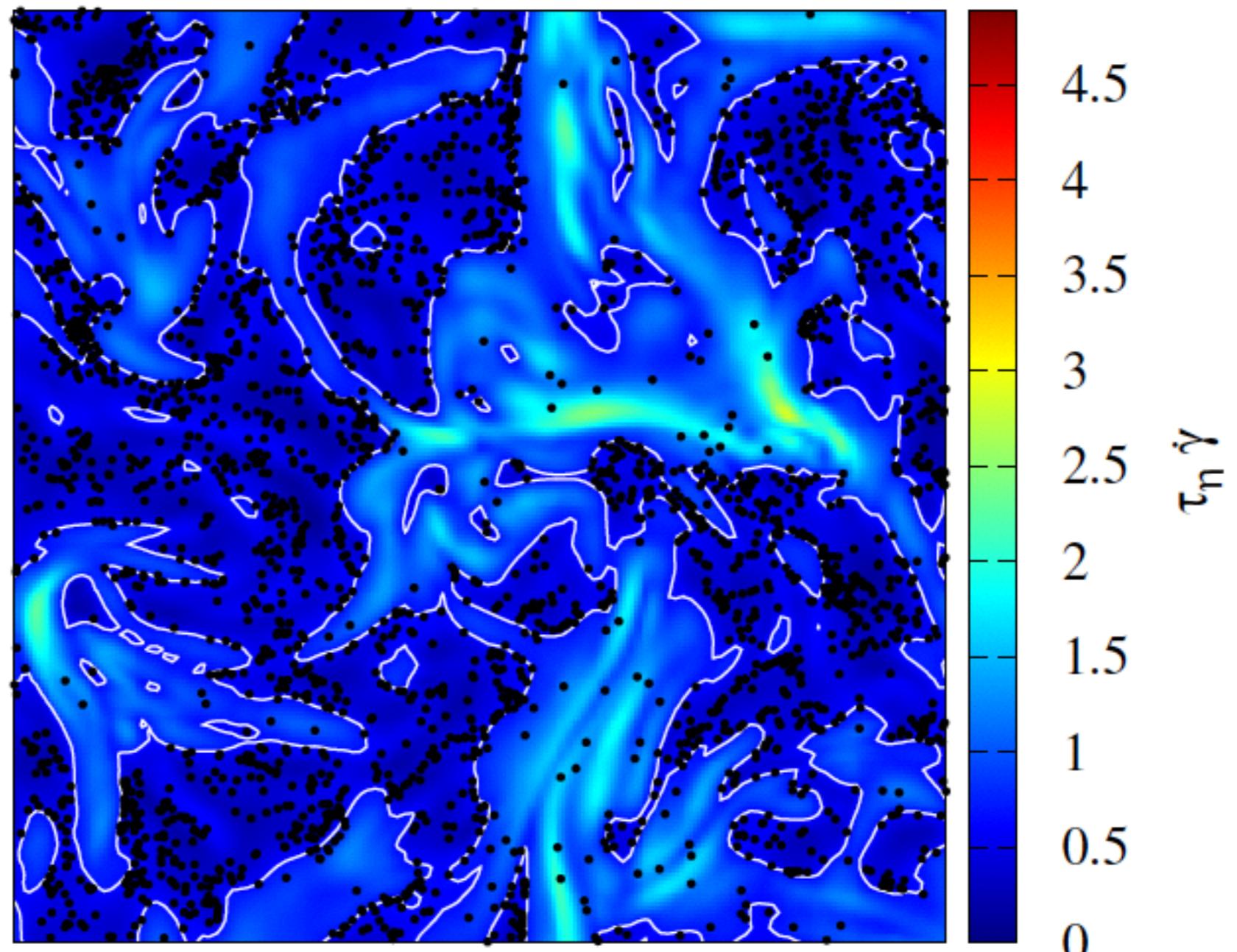
Spatial distribution

2D slice of thickness η , Jump intensity $u_J/u_\eta = 250$, $\tau_J = 10^{-2} \tau_\eta$

Jump shear-rate threshold

1) Low, many jumps, few dense islands

2) Intermediate,  efficient escape, sheet-like clusters



$$\tau_\eta \dot{\gamma}_T = 0.92$$



Spatial distribution

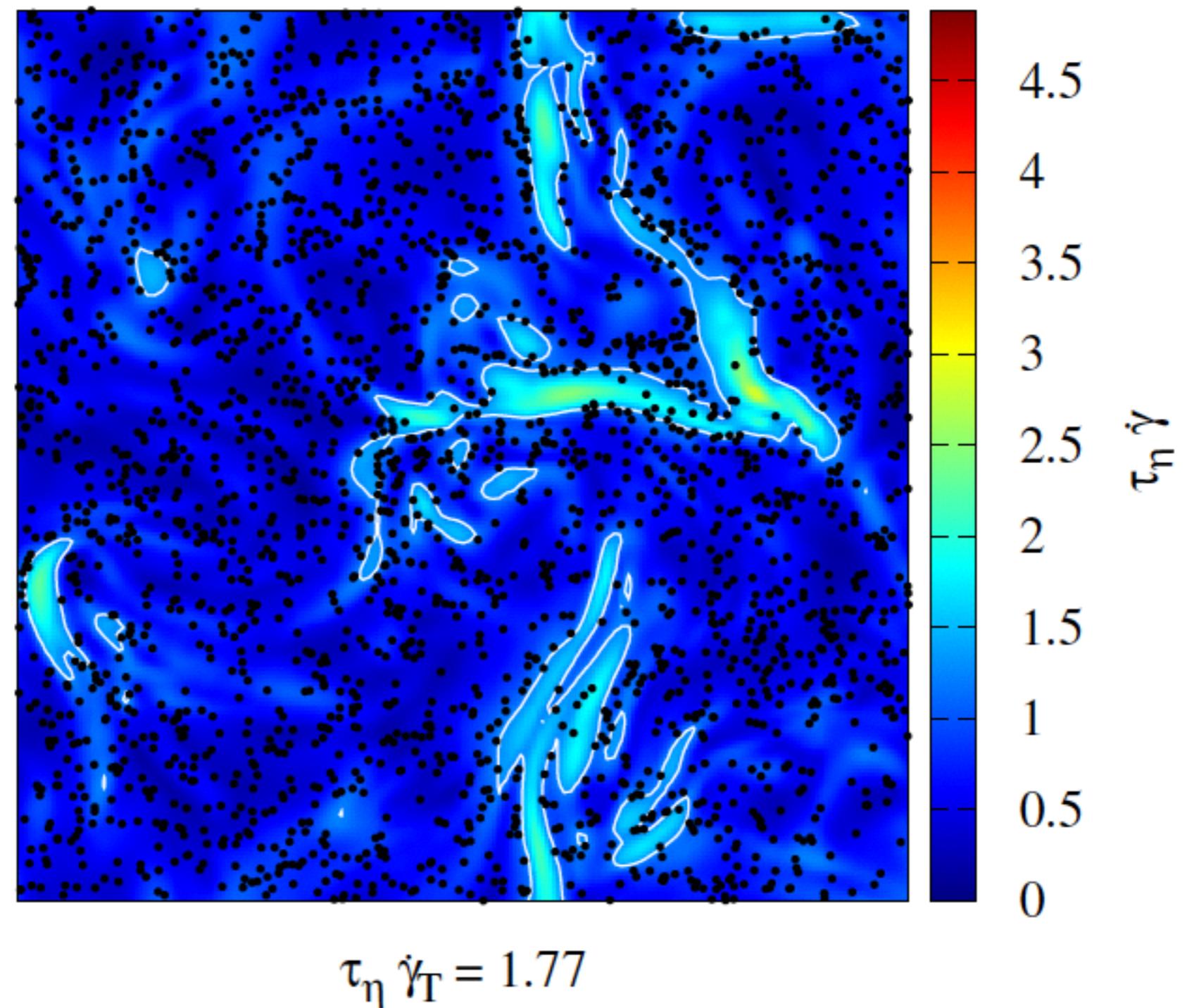
2D slice of thickness η , Jump intensity $u_J/u_\eta = 250$, $\tau_J = 10^{-2} \tau_\eta$

Jump shear-rate threshold

1) **Low**, many jumps, few dense islands

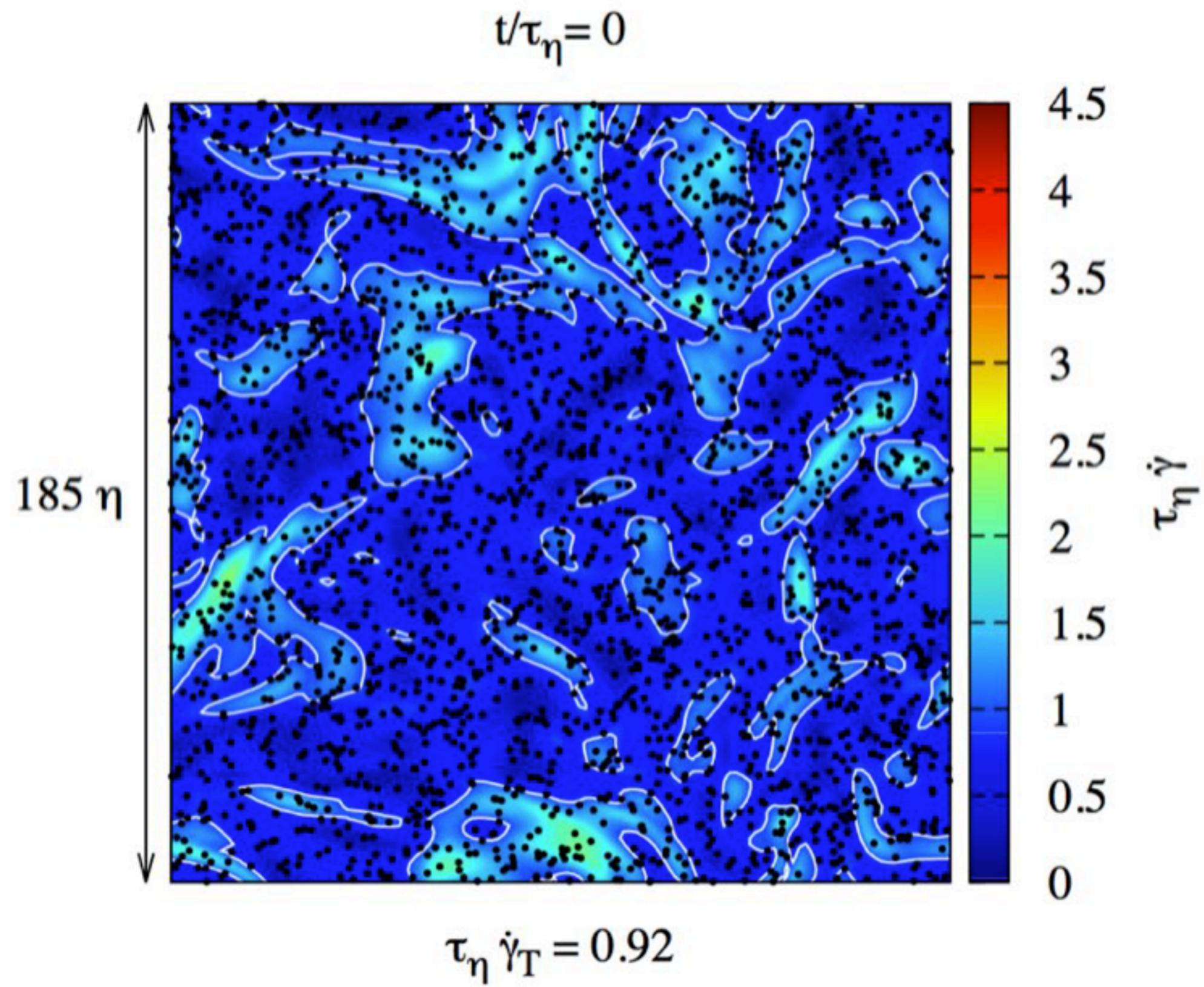
2) **Intermediate**, efficient escape, sheet-like clusters

3) **High**, efficient avoiding of extreme events, fading clusters



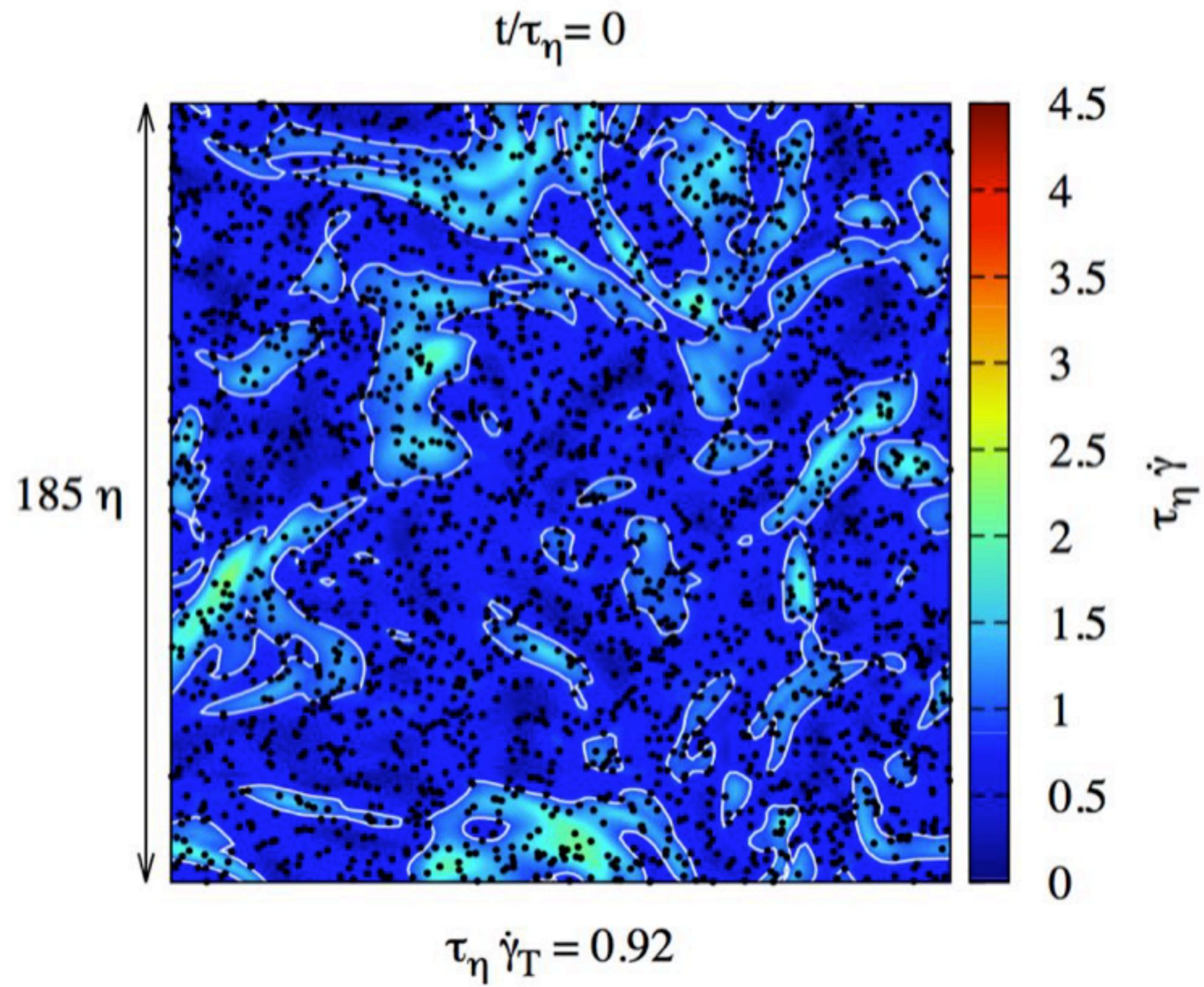


Movie





Movie



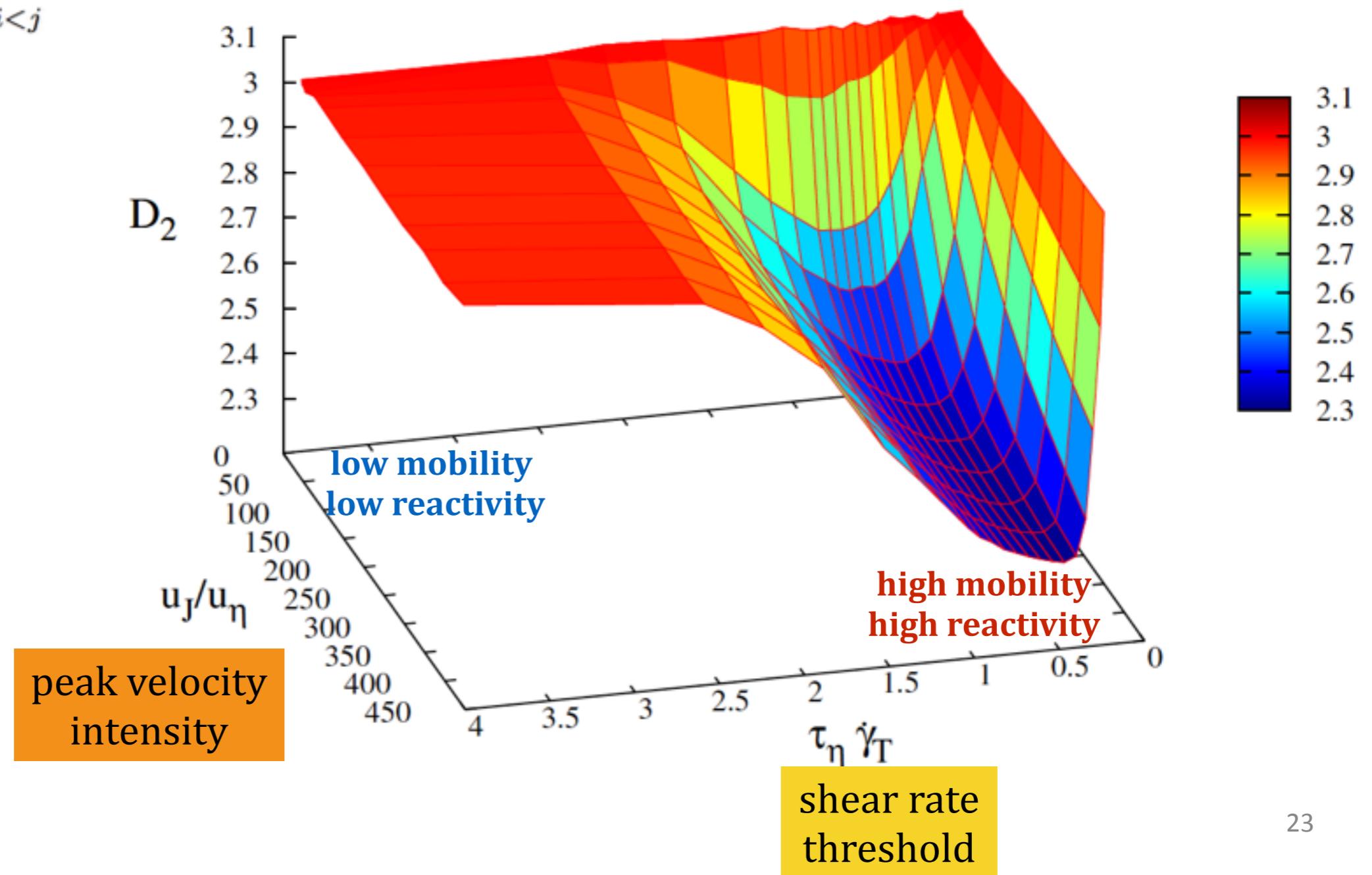


Correlation Dimension

Grassberger-Procaccia D_2

$$C(r) = \frac{2}{N(N-1)} \sum_{i < j} H(r - |X_i - X_j|)$$

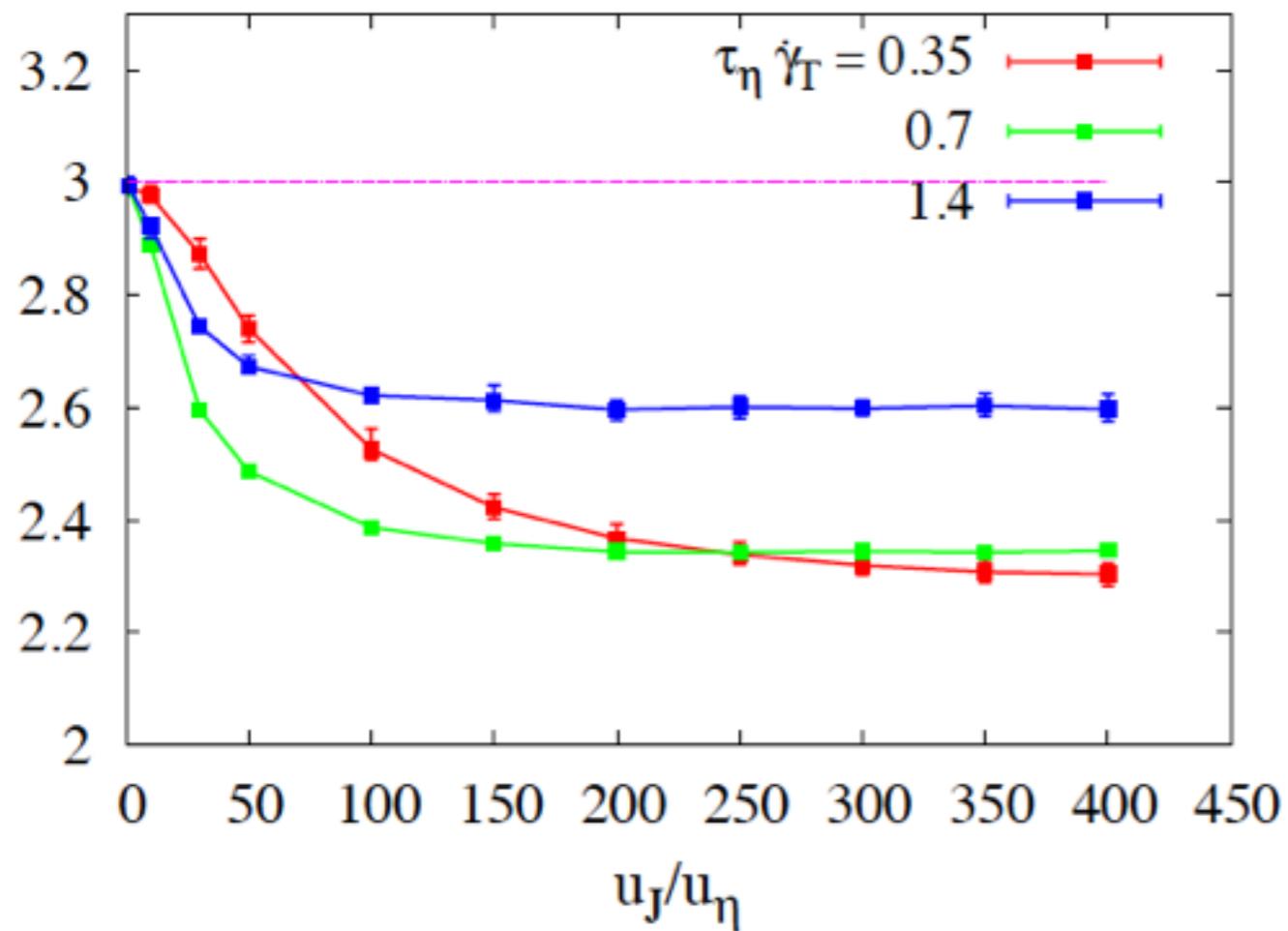
$$D_2 = \lim_{r \rightarrow 0} \frac{\log C(r)}{\log r}$$





Correlation Dimension

D_2 vs. peak velocity intensity



Saturation for huge values
of peak jump intensity

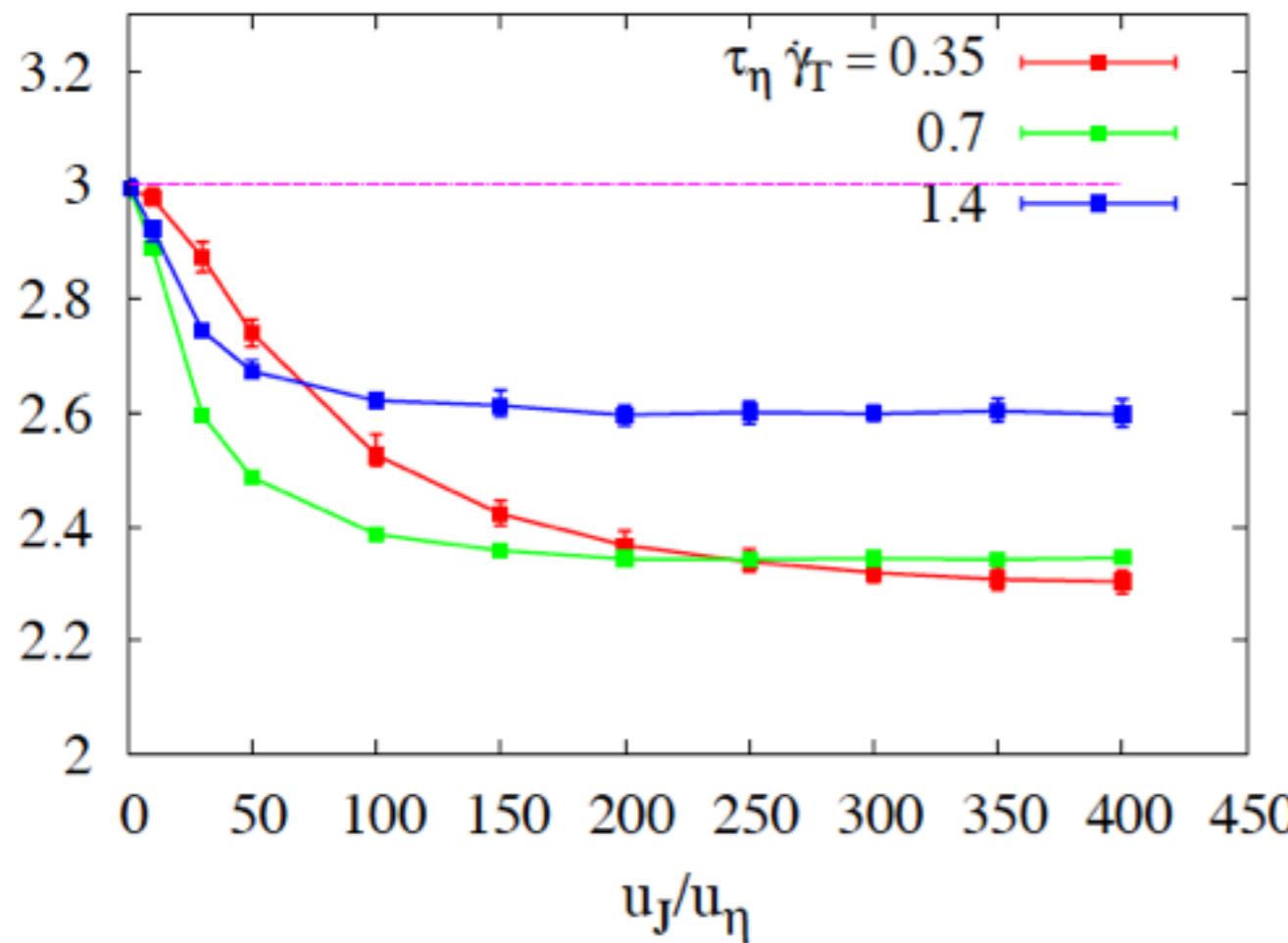
$$u_J > u_{rms} \sim 30 u_\eta$$



Correlation Dimension

D_2 vs.

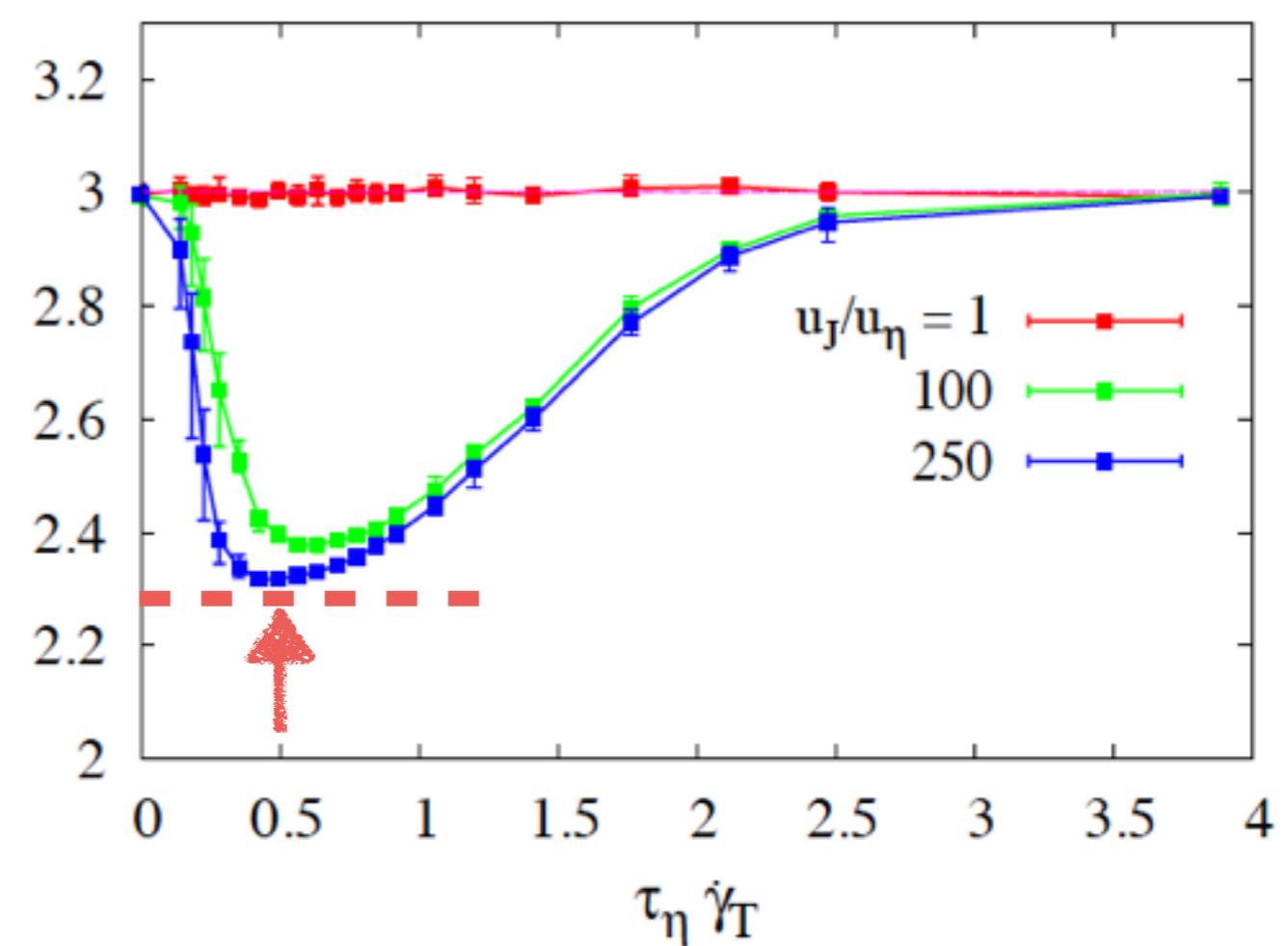
peak velocity
intensity



Saturation for huge values
of peak jump intensity
 $u_J > u_{rms} \sim 30 u_\eta$

D_2 vs.

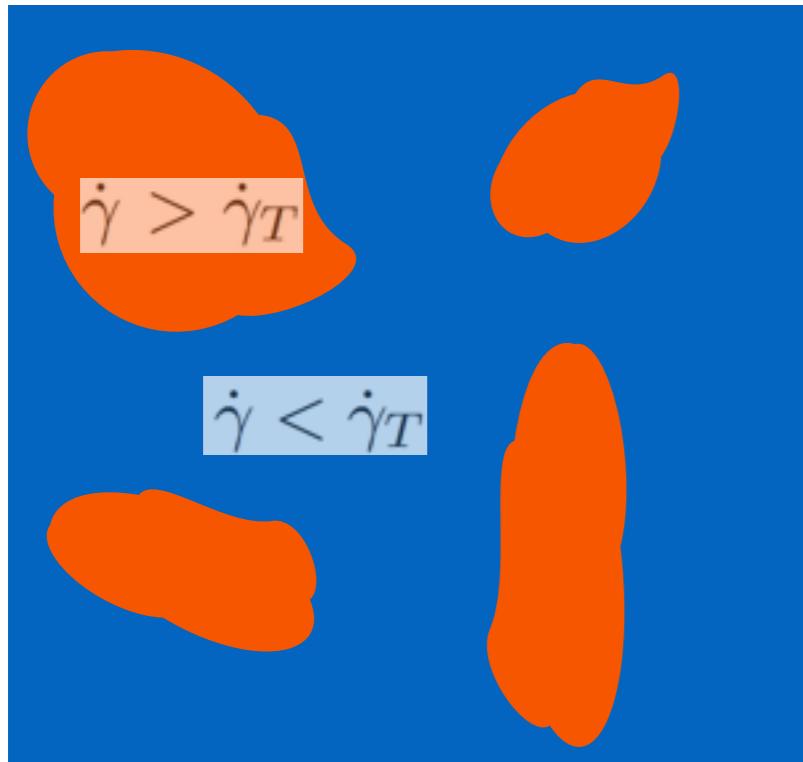
shear rate
threshold



Optimal threshold value
why?

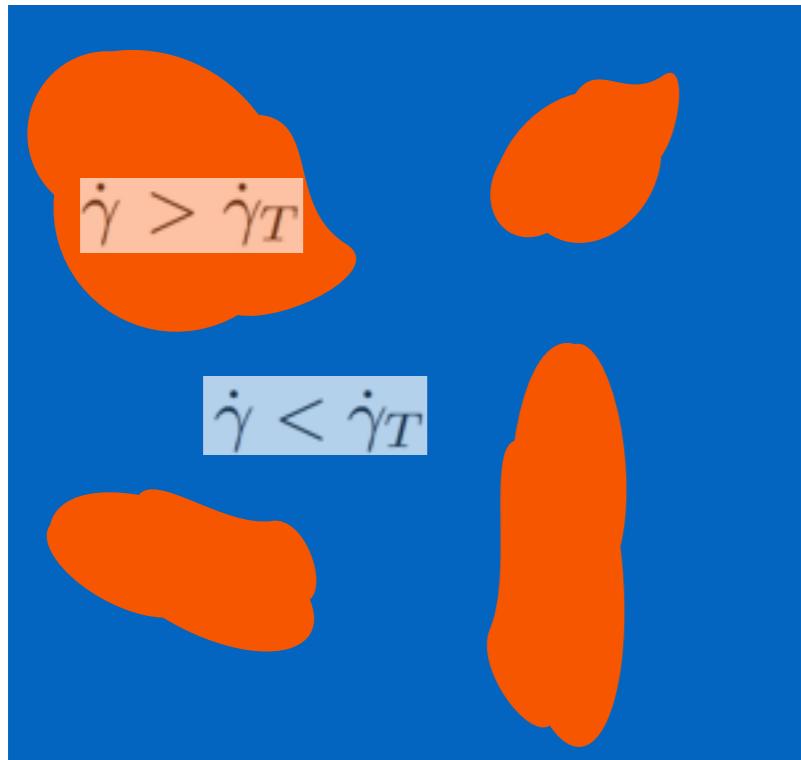


Clustering mechanism (1)





Clustering mechanism (1)



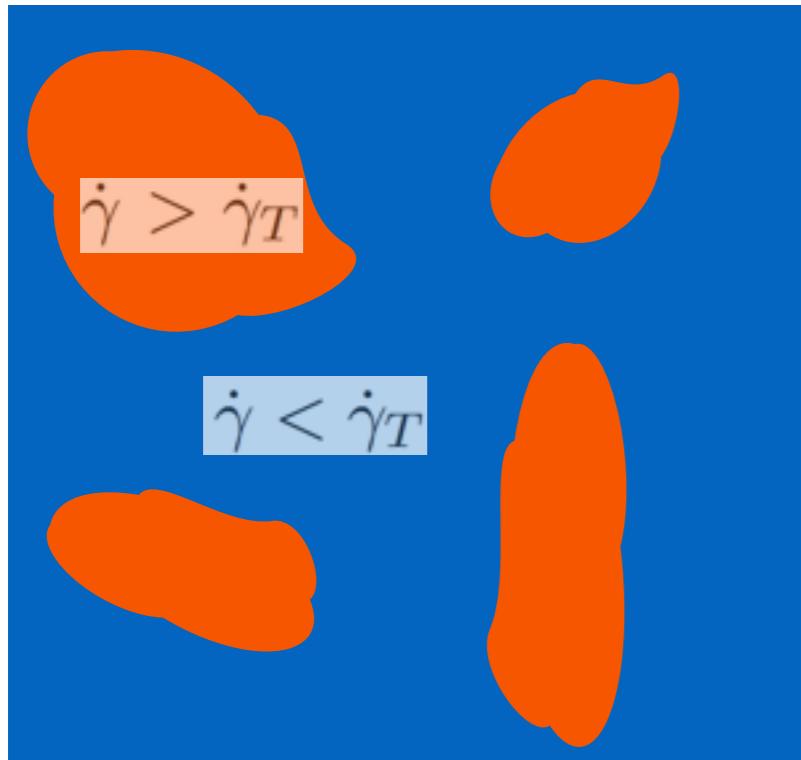
1) Probability of a successful jump

$$\sim \mathcal{V}_{\dot{\gamma} < \dot{\gamma}_T}$$

volume of
comfort regions



Clustering mechanism (1)



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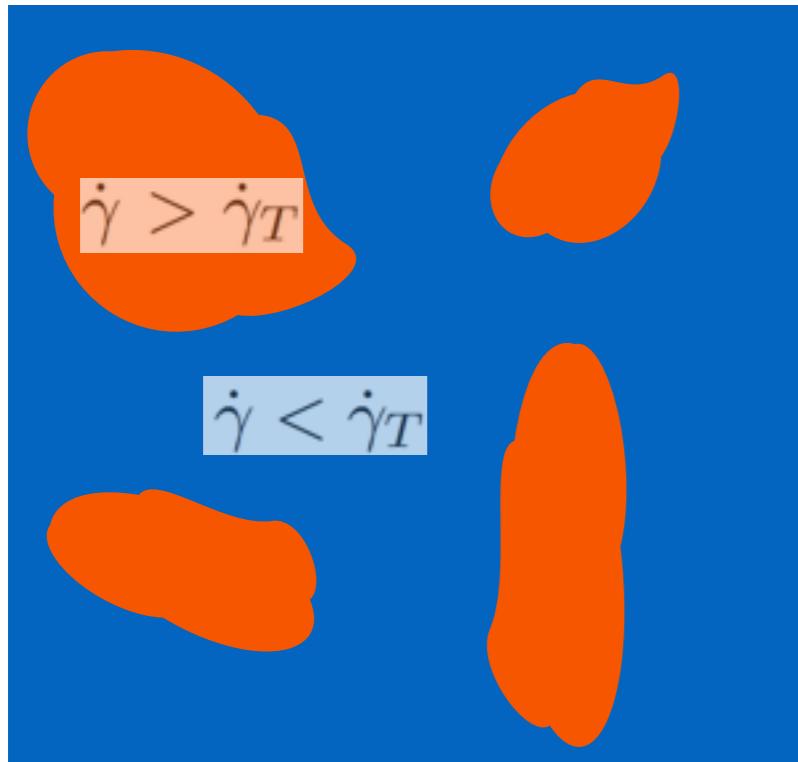
2) Rate of jumps

$$\sim \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T}$$

volume of
alert regions



Clustering mechanism (1)



1) Probability of a successful jump

$$\sim \mathcal{V}_{\dot{\gamma} < \dot{\gamma}_T}$$

volume of
comfort regions

2) Rate of jumps

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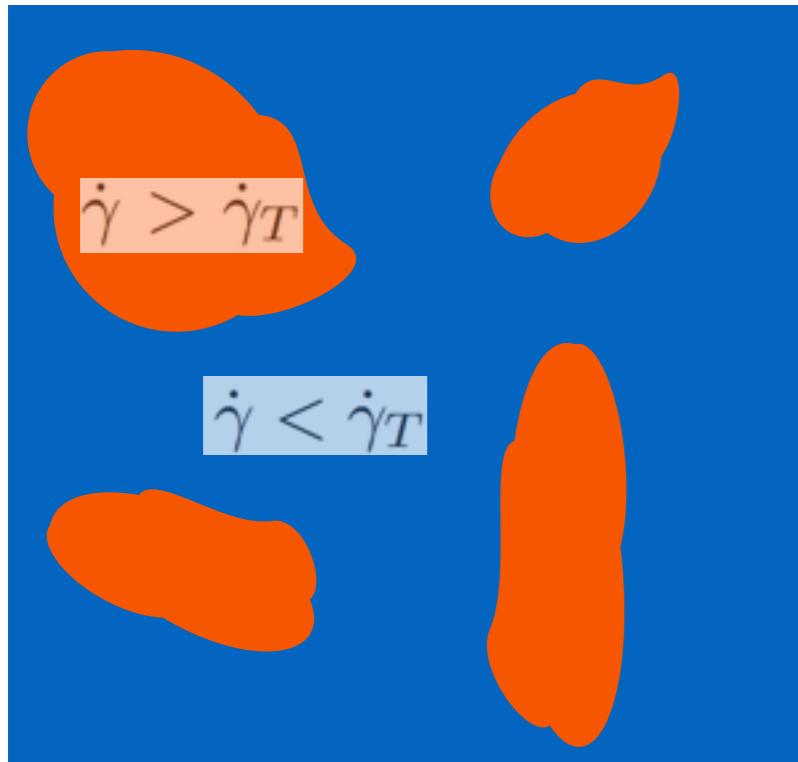
3) Clustering

$$\sim \mathcal{V}_{\dot{\gamma} < \dot{\gamma}_T} \cdot \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T}$$

$$= \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T} \cdot (\mathcal{V}_{tot} - \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T})$$



Clustering mechanism (1)



1) Probability of a successful jump

$$\sim \mathcal{V}_{\dot{\gamma} < \dot{\gamma}_T}$$

volume of
comfort regions

2) Rate of jumps

$$\sim \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T}$$

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alert regions

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$$\sim \mathcal{V}_{\dot{\gamma} < \dot{\gamma}_T} \cdot \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T}$$

$$= \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T} \cdot (\mathcal{V}_{tot} - \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T})$$

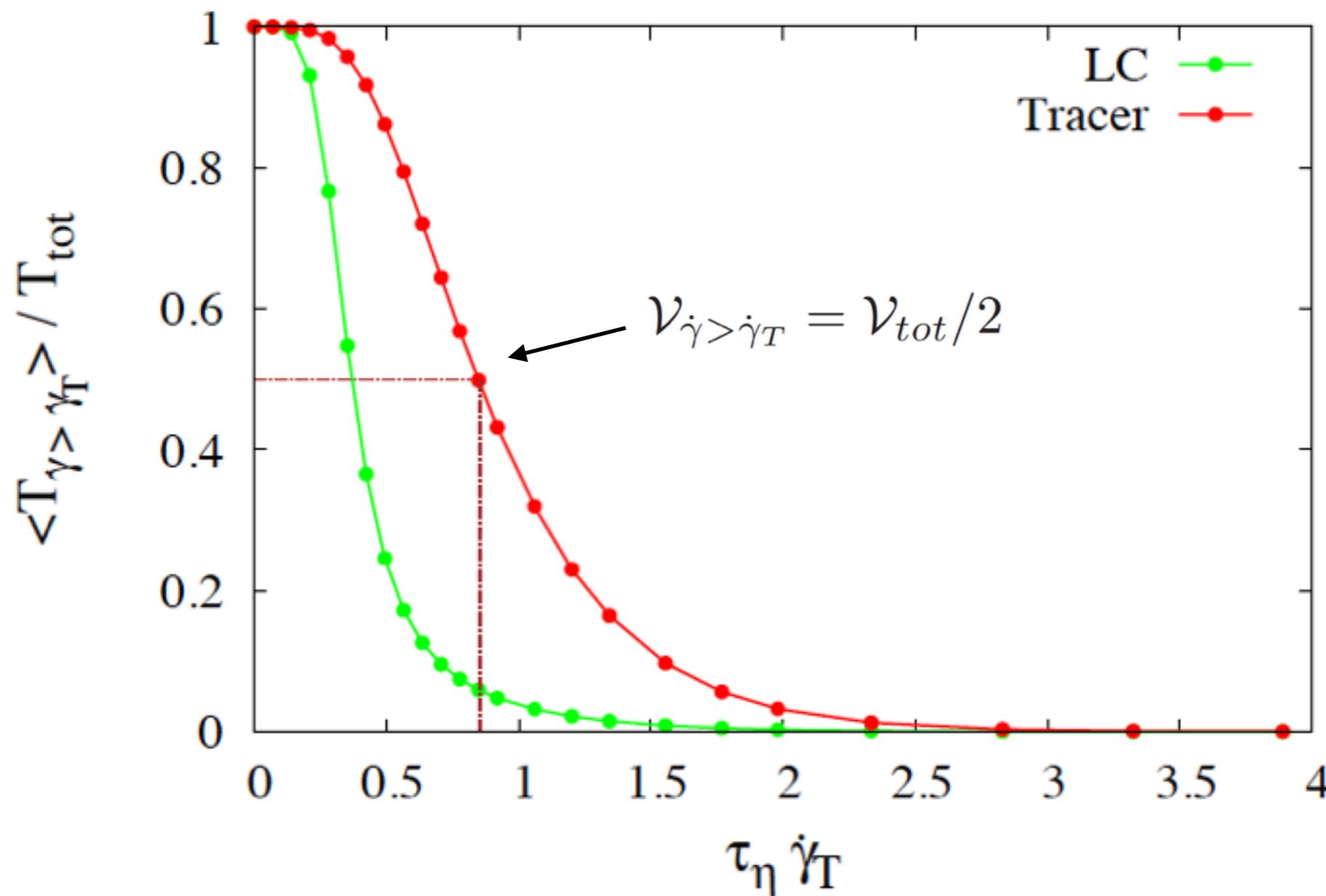
Maximum for

$$\mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T} = \mathcal{V}_{tot}/2$$

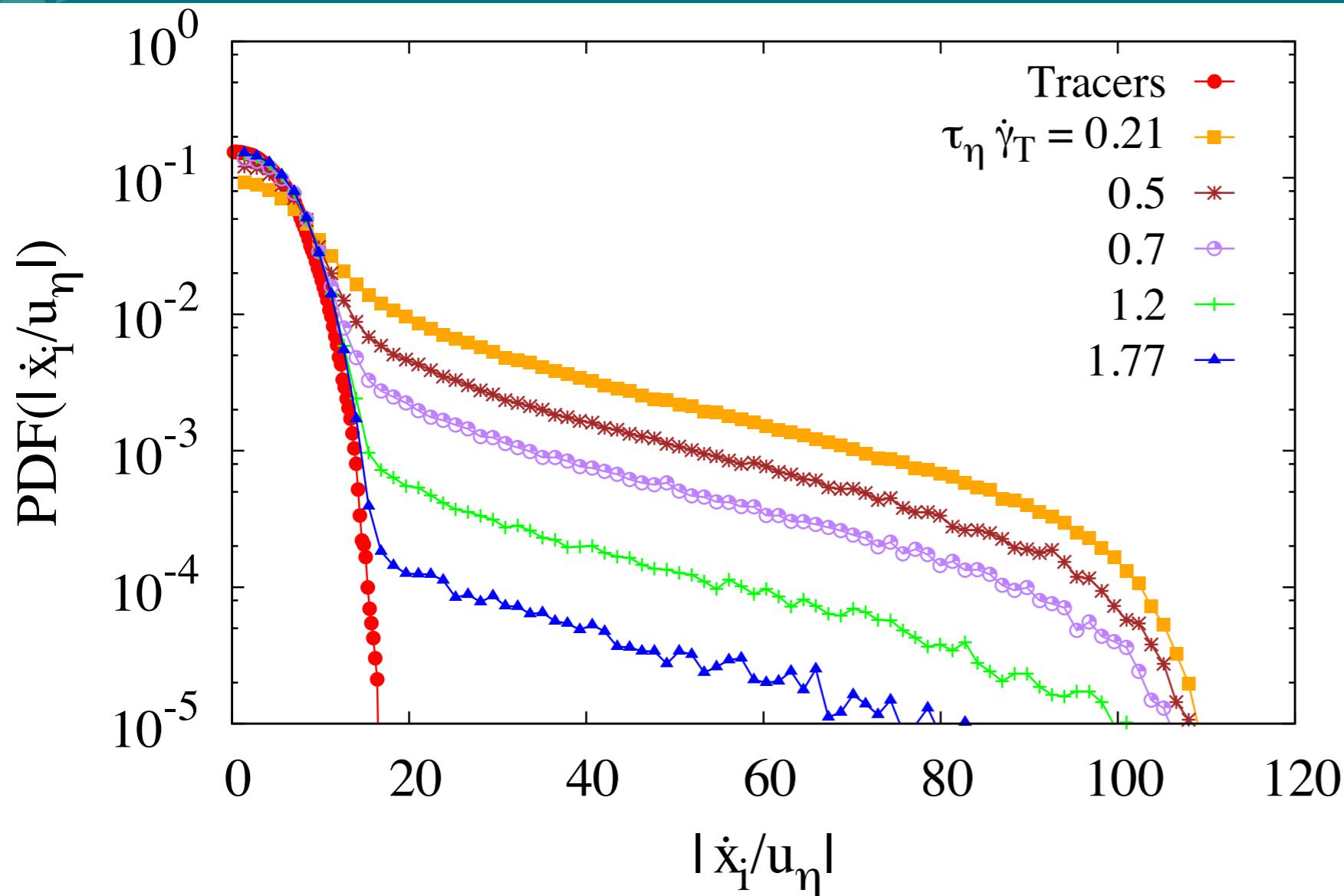


Clustering mechanism (2)

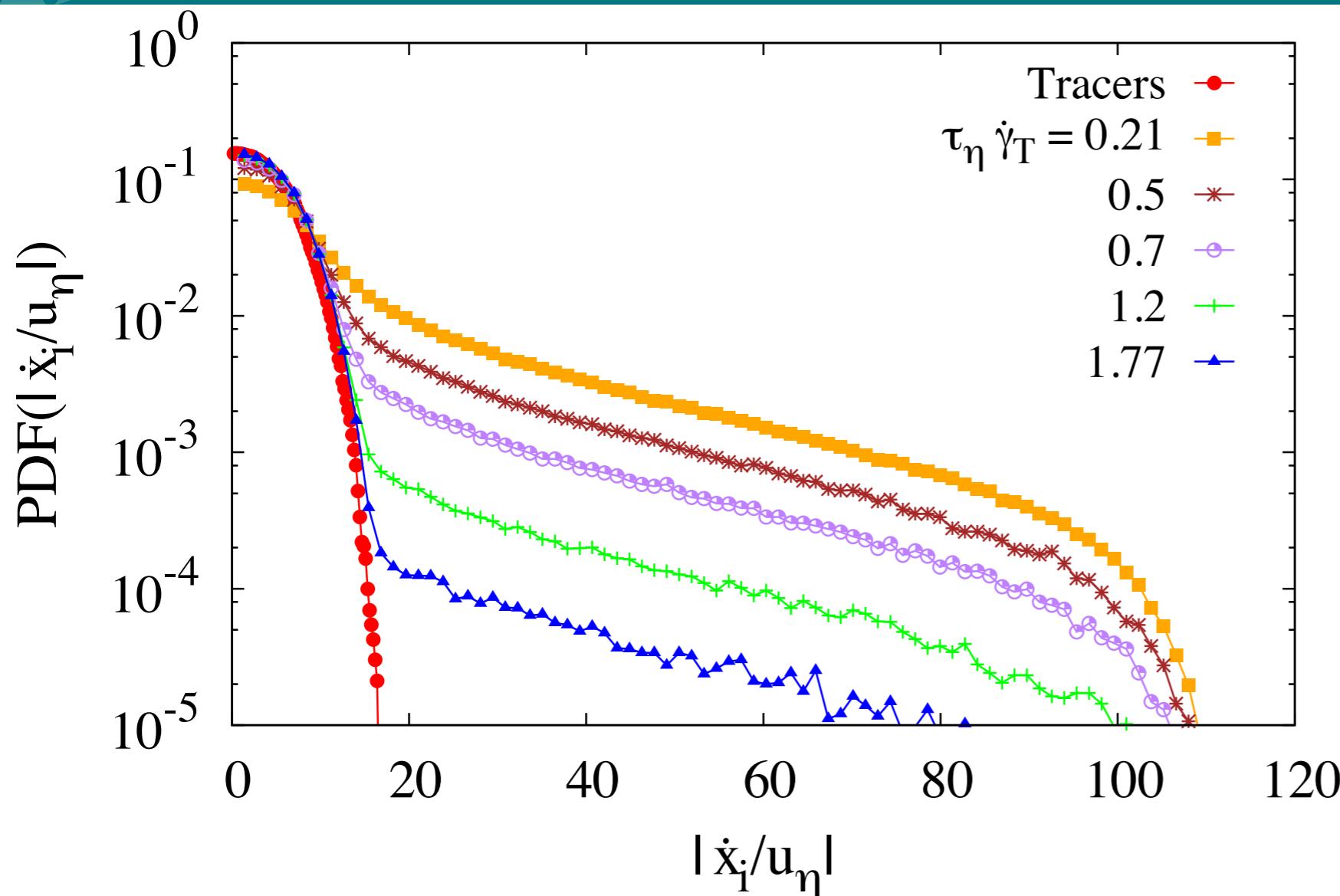
Fraction of time Time spent in **alert regions** $\dot{\gamma} > \dot{\gamma}_T$



PDF of Velocity



PDF of Velocity



$$\dot{\mathbf{x}} = \mathbf{U} + \alpha \ p \ u_J e^{-t/\tau_J}$$

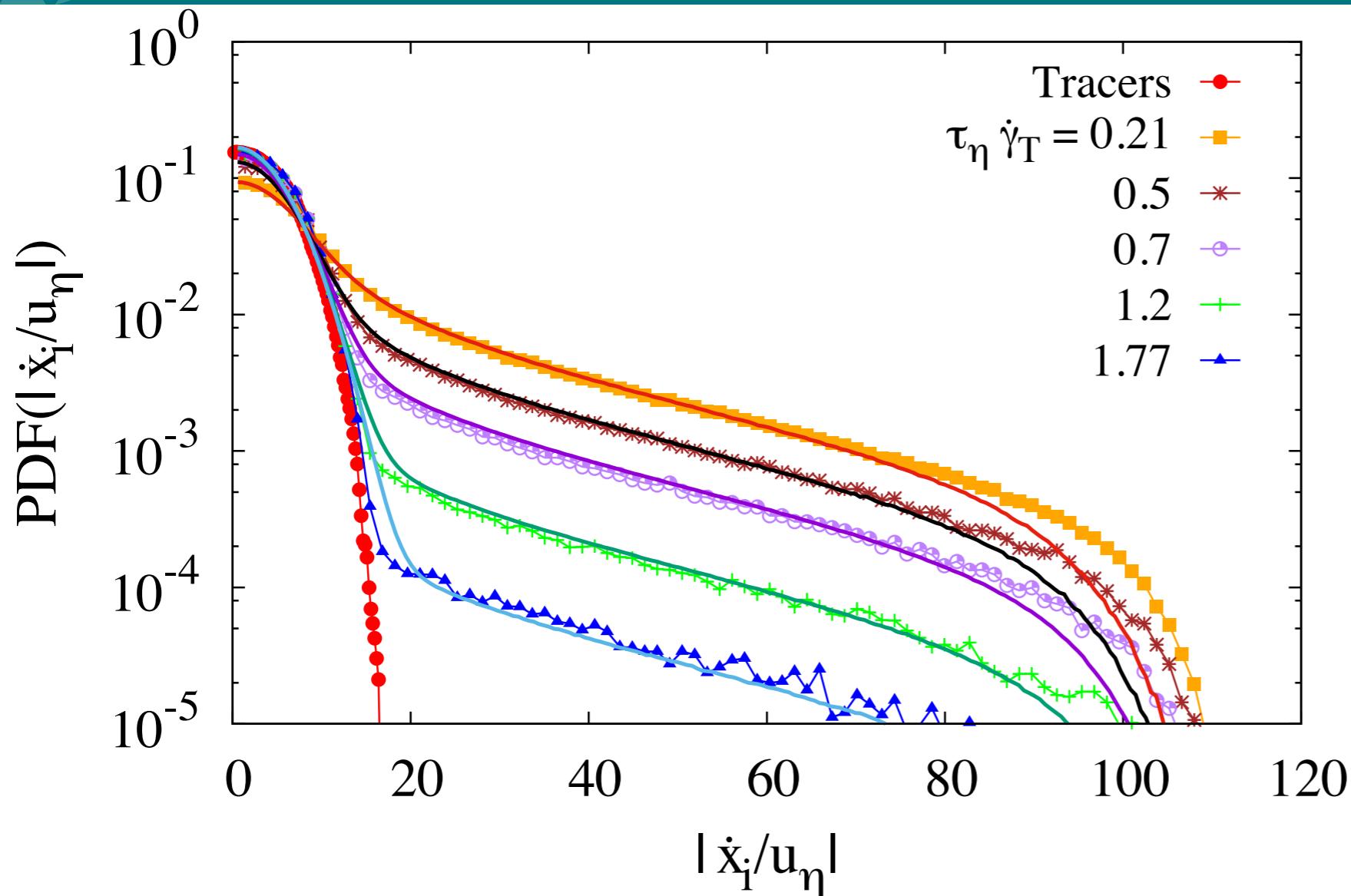
Gaussian random variable

jumping fraction?

random vector

flat random $[0, t_e]$

PDF of Velocity



$$\dot{\mathbf{x}} = \mathbf{U} + \alpha \ p \ u_J e^{-t/\tau_J}$$

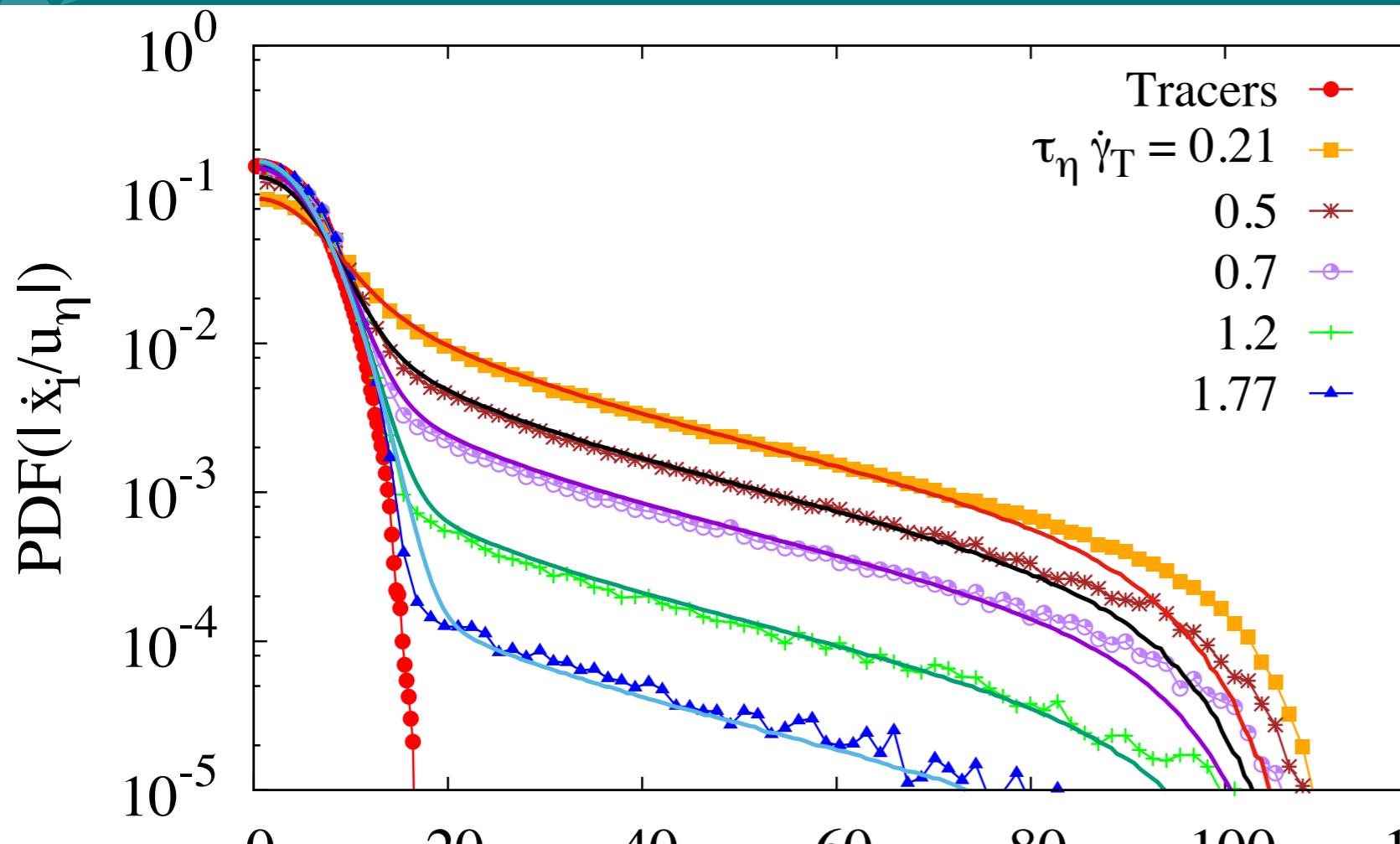
Gaussian random variable

jumping fraction?

random vector

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PDF of Velocity



$$\dot{x} = \mathbf{U} + \alpha p u_J e^{-t/\tau_J}$$

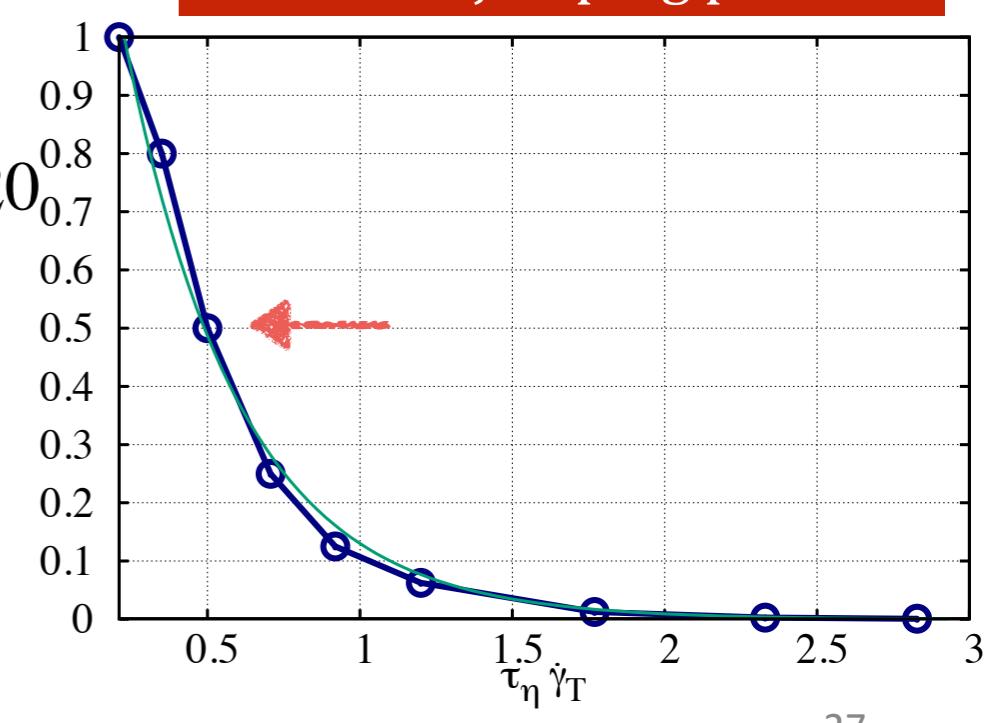
Gaussian random variable

jumping fraction?

random vector

flat random $[0, t_e]$

Deduced α
fraction of jumping particles



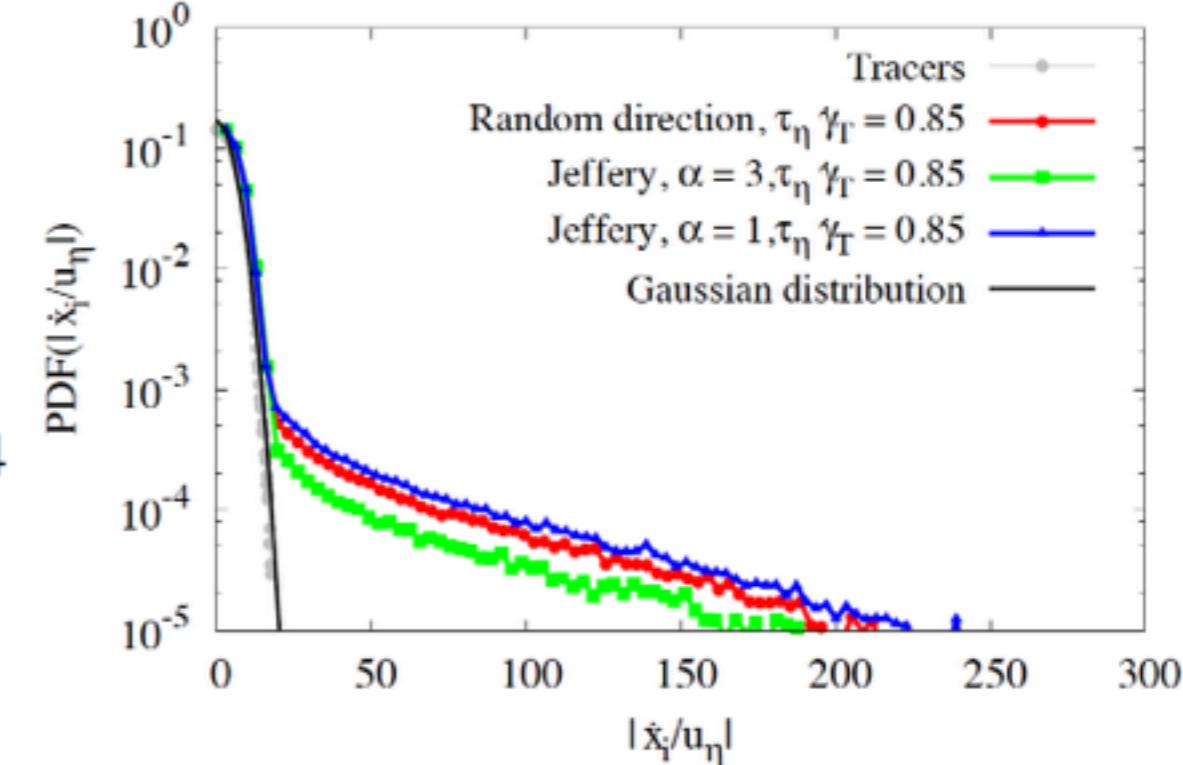
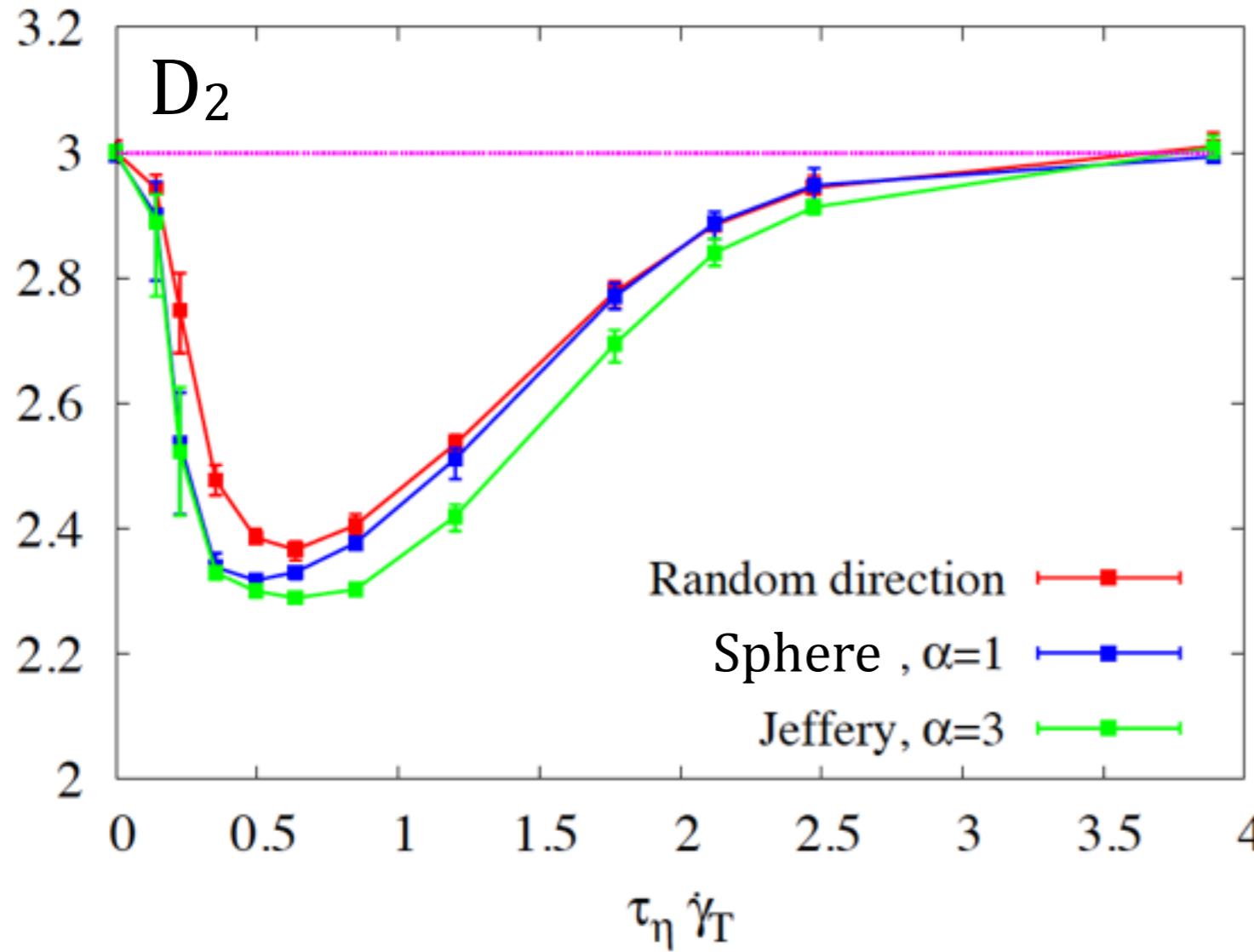


Summary

- LC model exhibits clustering in turbulence $D_2 \sim 2.3$
- Necessary conditions for Clustering:
 - 1) **high jump speed** $u_j > u_{rms}$
 - 2) **sharp sensitivity to shear rate** $O(\tau_\eta^{-1})$
- Clustering comes from **inhomogeneity** rather than anisotropy of the model
(Excluded volume mechanism)
- Different mechanism from the one identified for motile algae (gyrotaxis induced).

LC Model v1.0
Many possible extensions...

Effect of Aspect ratio

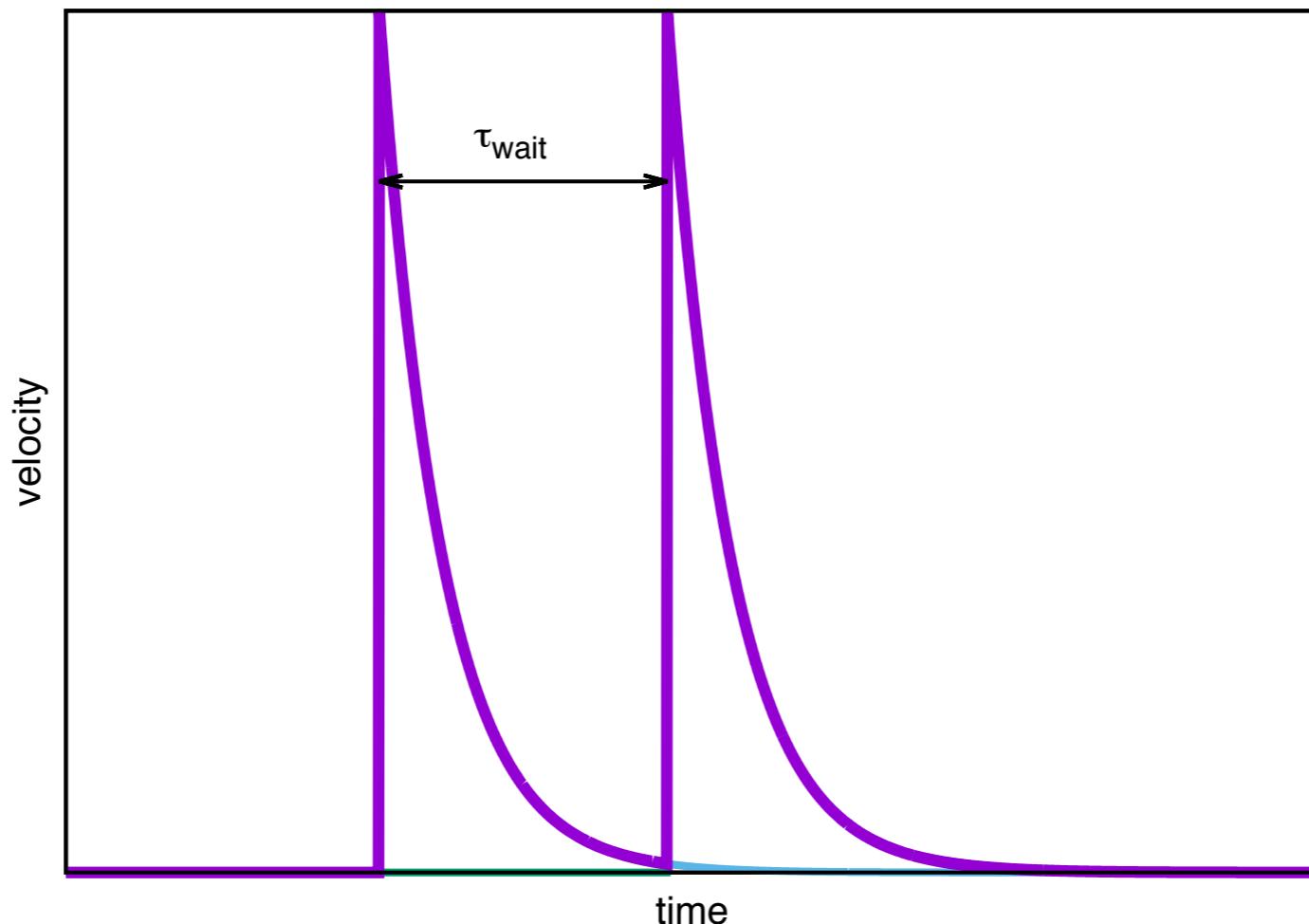


Particle orientation dynamics
no impact on clustering
or velocity distribution



Effect of jump time latency

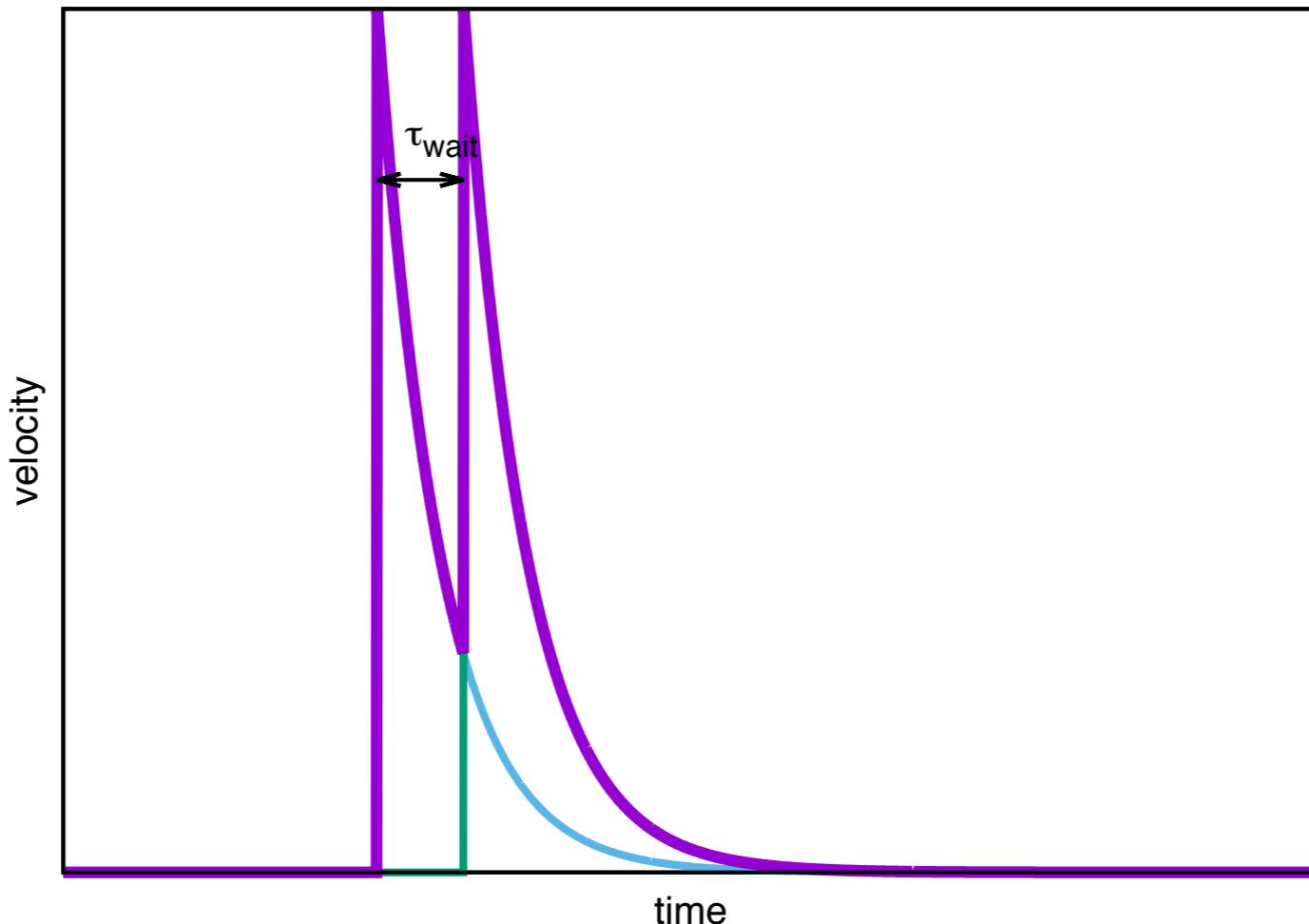
What if one varies $t_e - t_i = \tau_{\text{wait}}$?





Effect of jump time latency

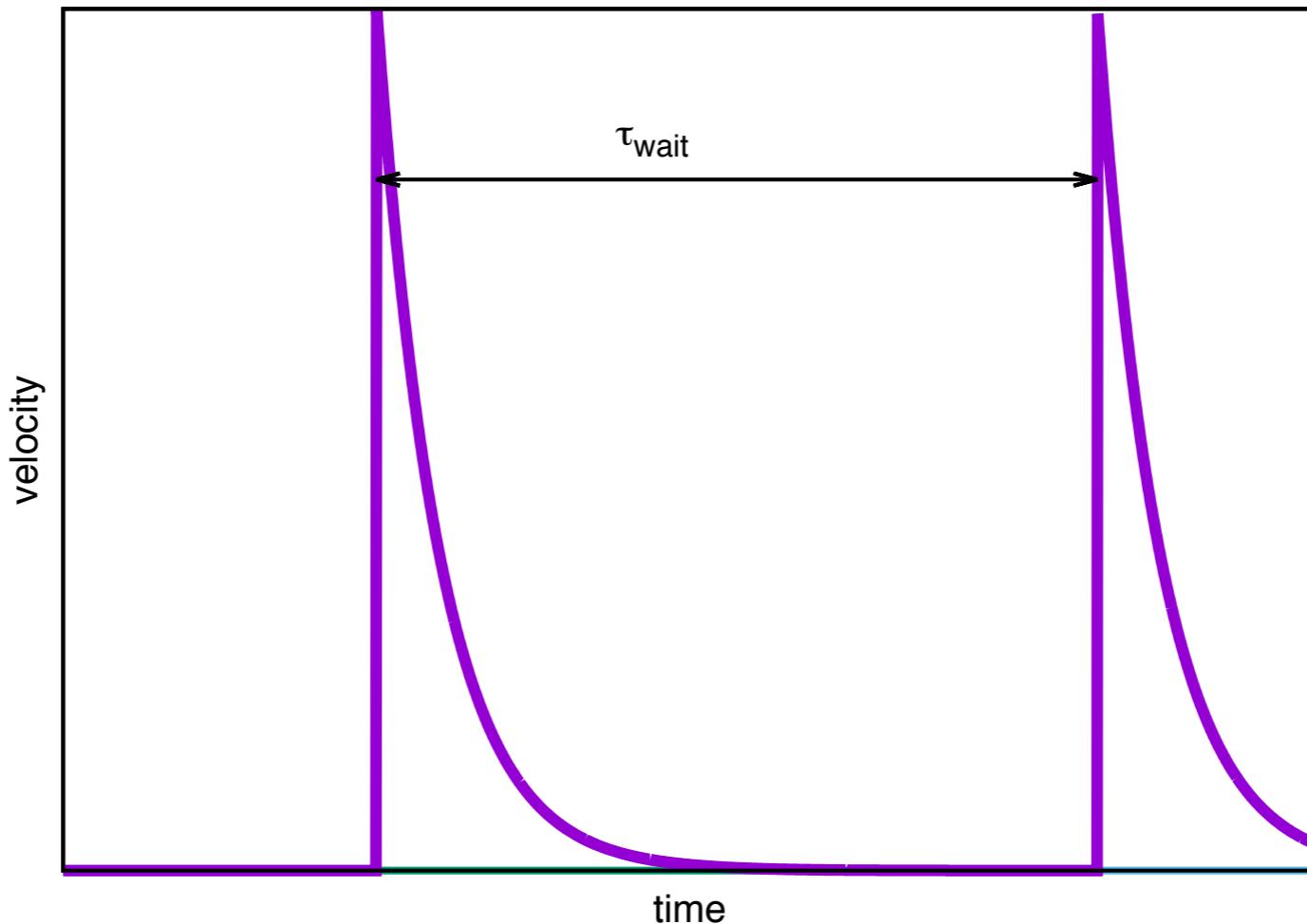
What if one varies $t_e - t_i = \tau_{\text{wait}}$?





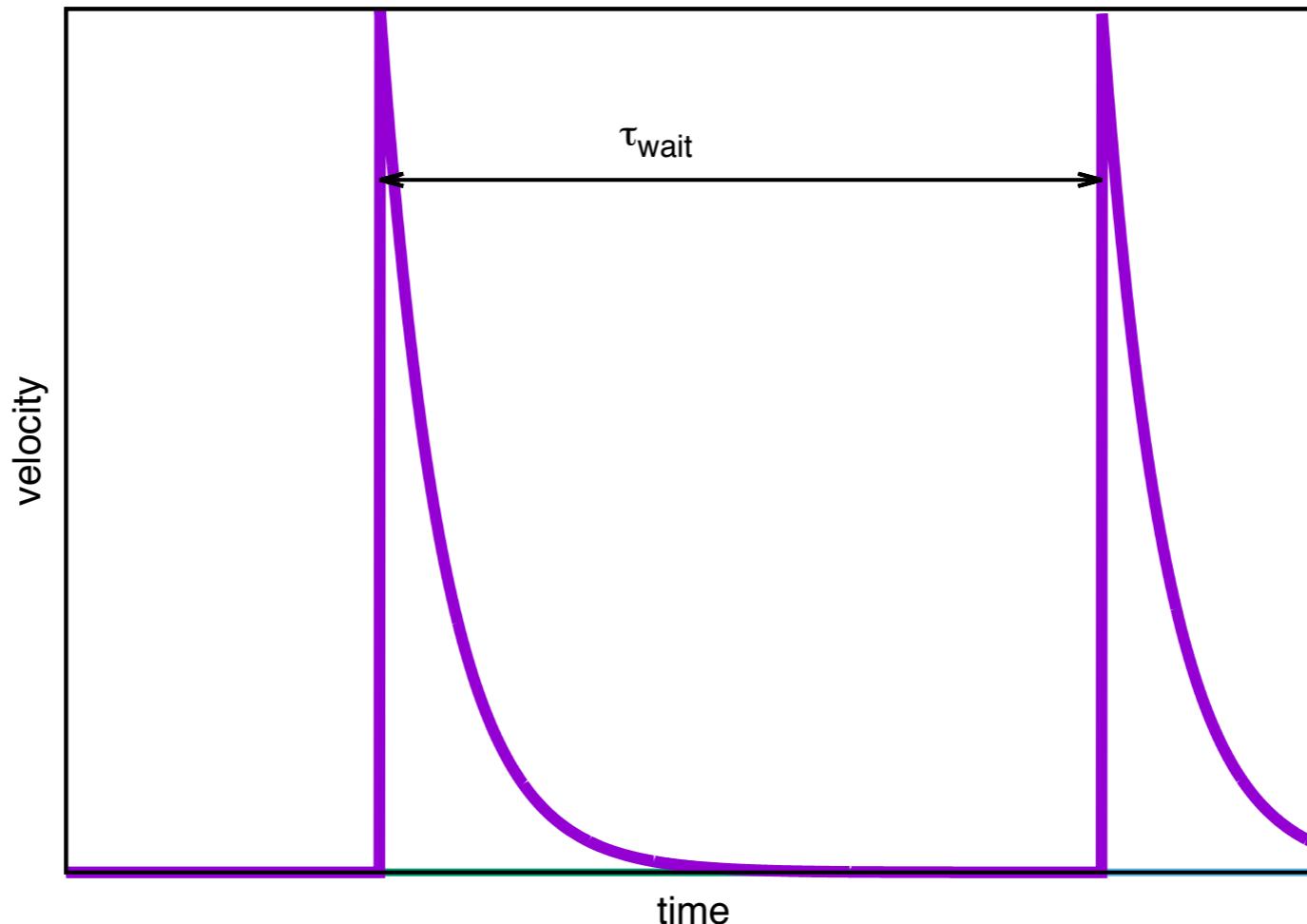
Effect of jump time latency

What if one varies $t_e - t_i = \tau_{\text{wait}}$?



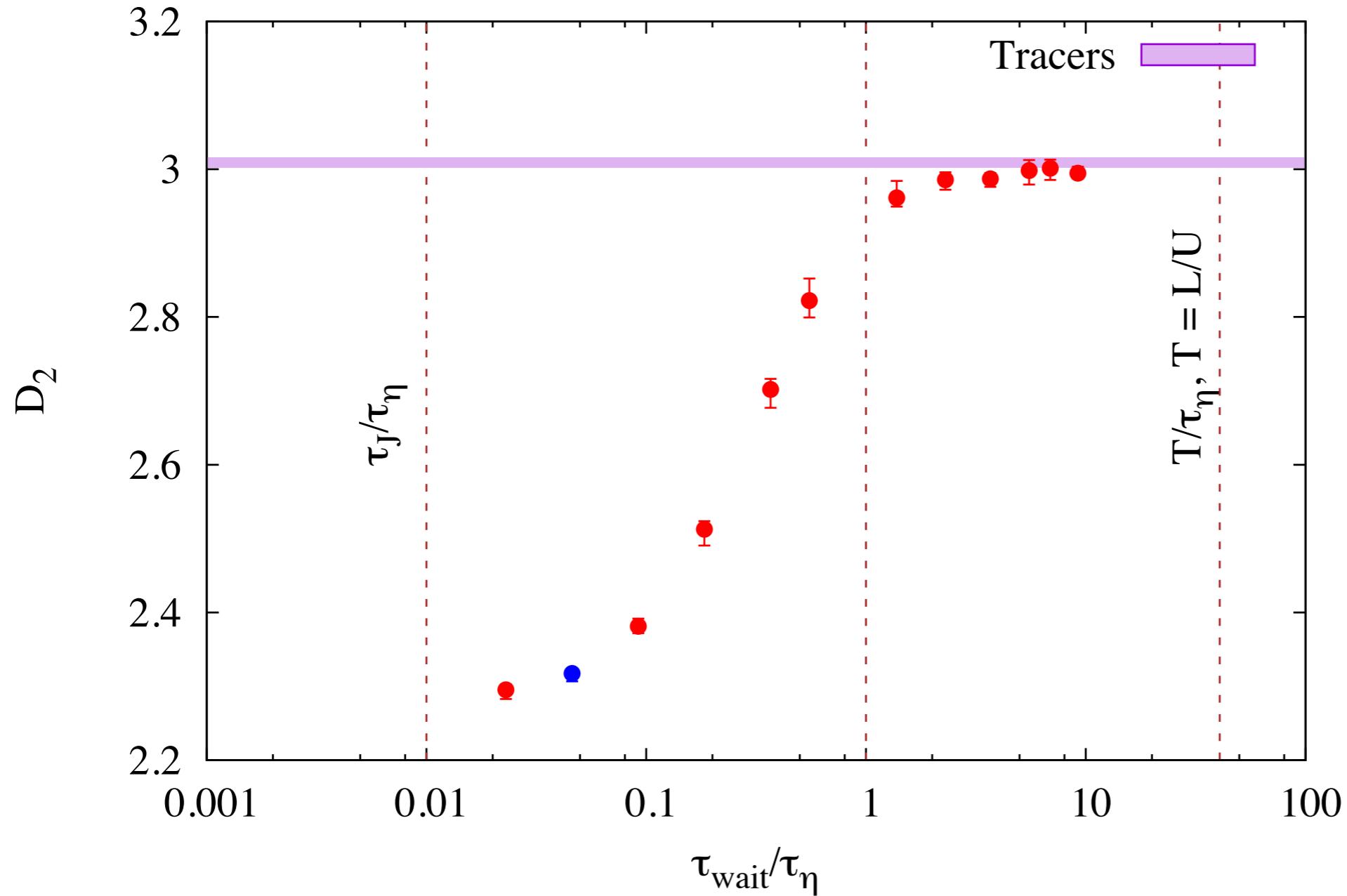
Effect of jump time latency

What if one varies $t_e - t_i = \tau_{\text{wait}}$?



Which effect on clustering?

Effect of jump time latency (2)

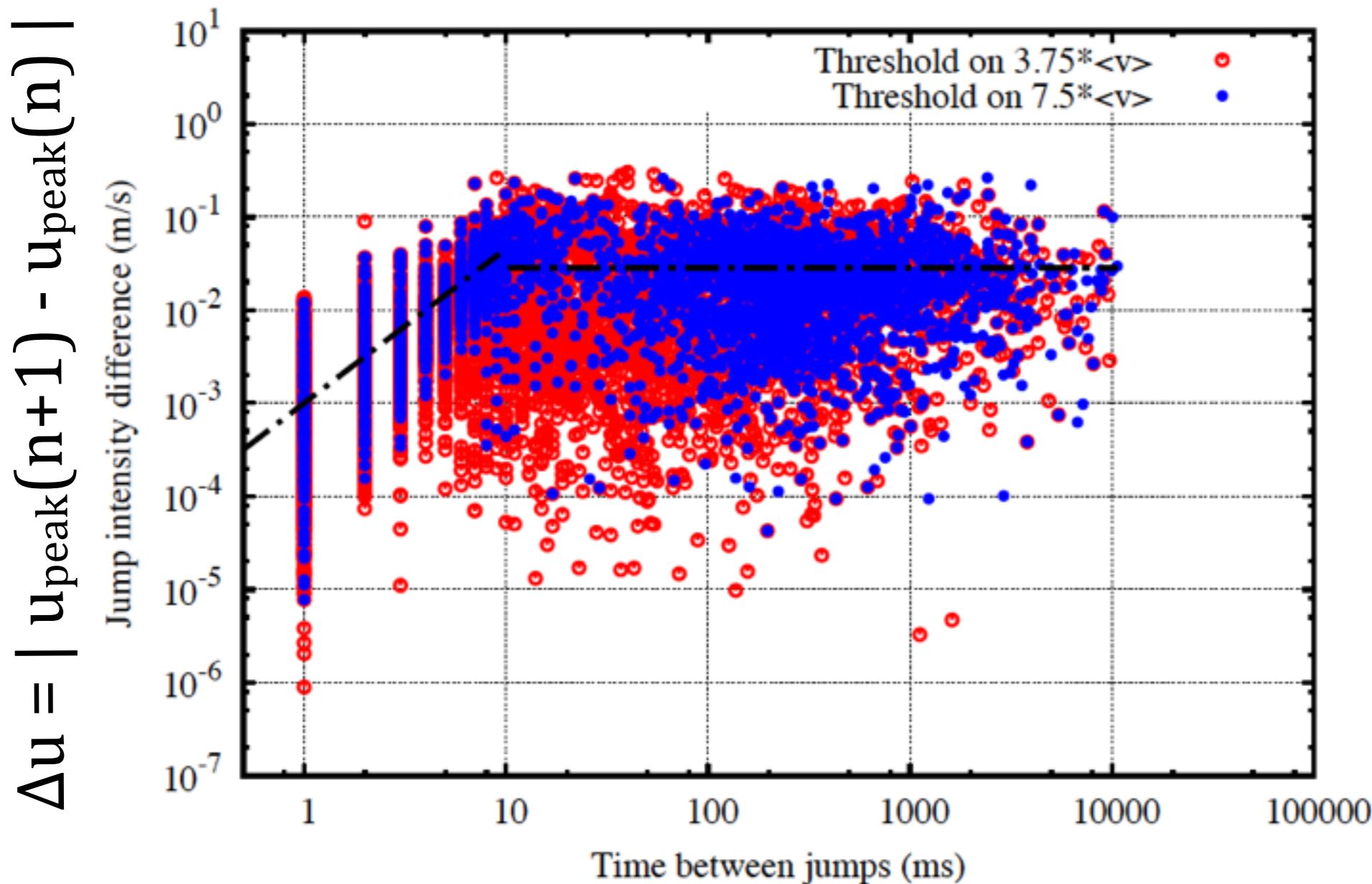


Only a prompt reaction leads to clusters



Jump intensity vs latency in experimental data

Correlation: time gap with peak velocity gap

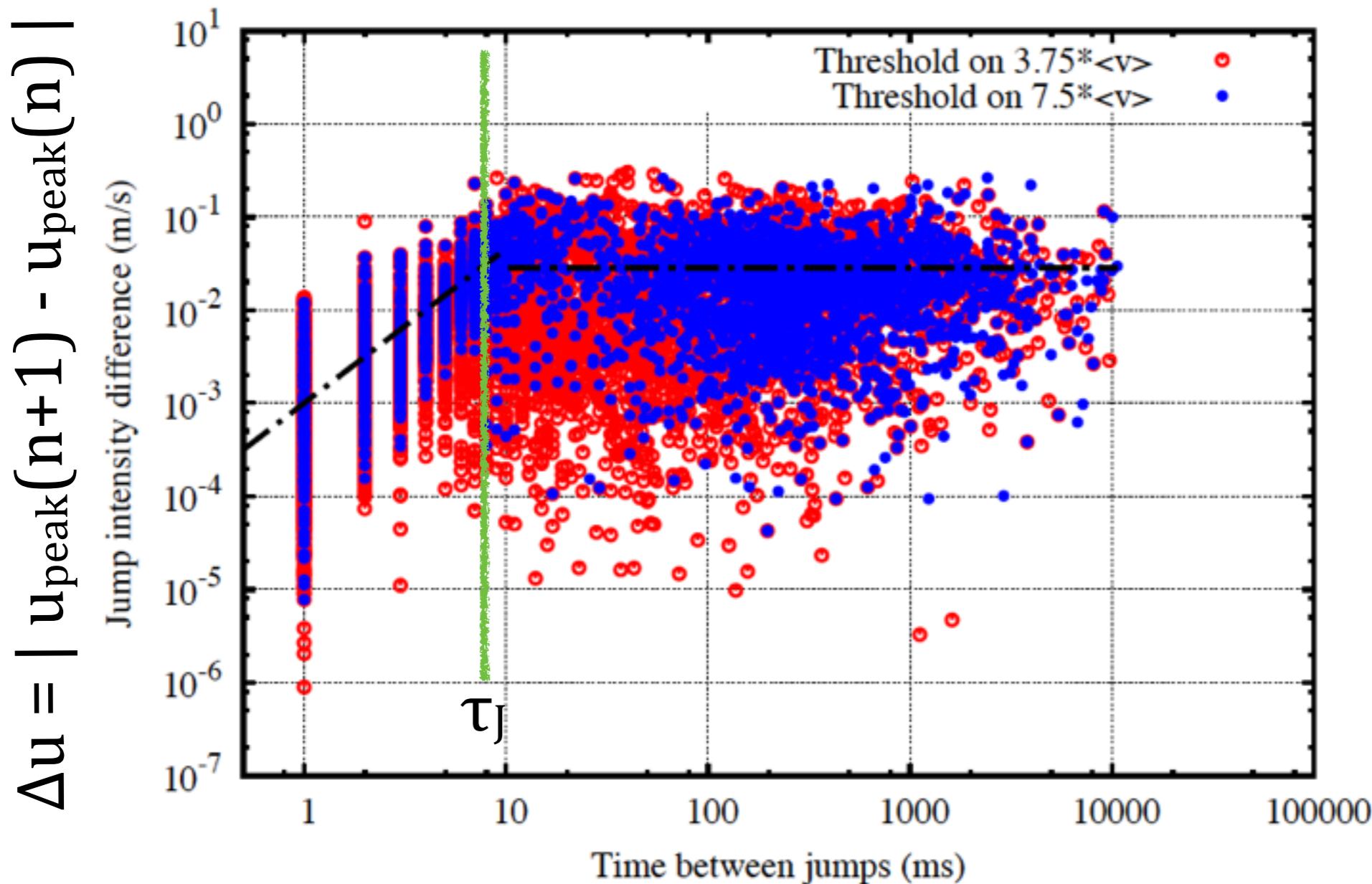


$$\Delta t = t_{\text{jump}}(n+1) - t_{\text{jump}}(n)$$



Jump intensity vs latency in experimental data

Correlation: time gap with peak velocity gap



$$\Delta t = t_{\text{jump}}(n+1) - t_{\text{jump}}(n)$$



Conclusions & Perspectives

- Necessary conditions for Clustering:
 - 1) **high jump speed** $u_j > u_{rms}$
 - 2) **sharp sensitivity to shear rate** $O(\tau_\eta^{-1})$
 - 3) **high jump frequency** $\ll \tau_\eta$
- If reaction is quick, particle orientation is not a crucial aspect
- Eulerian modelling should be possible in these conditions

Effective Diffusivity(local share-rate)

[arXiv:1601.01438

A Lagrangian model of Copepod dynamics: clustering by escape jumps in turbulence
Hamidreza Ardestiri, Ibtissem Benkreddad, François G. Schmitt, Sami Souissi, Federico Toschi, Enrico Calzavarini



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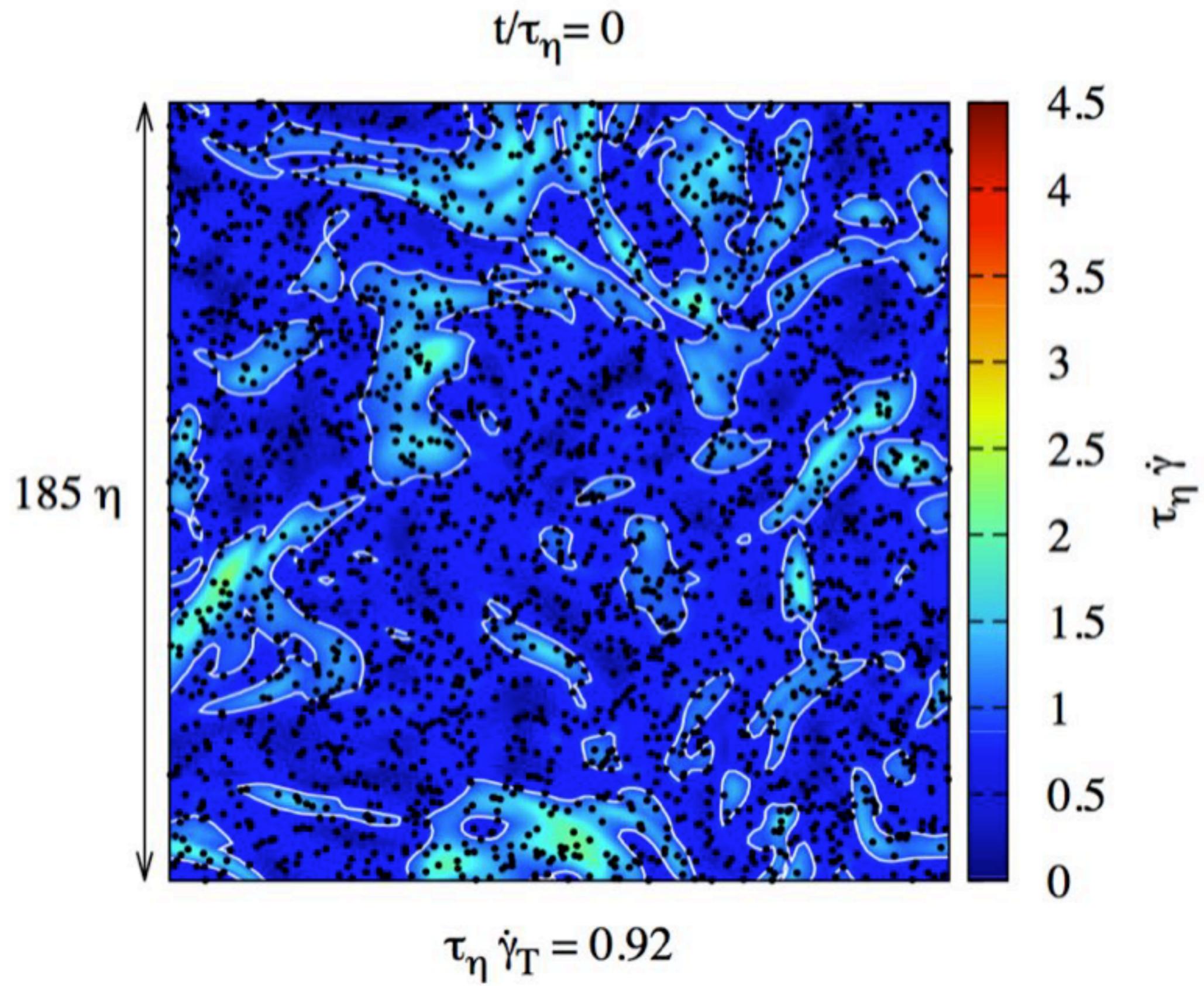
Effective Diffusivity(local share-rate)

Model refinements

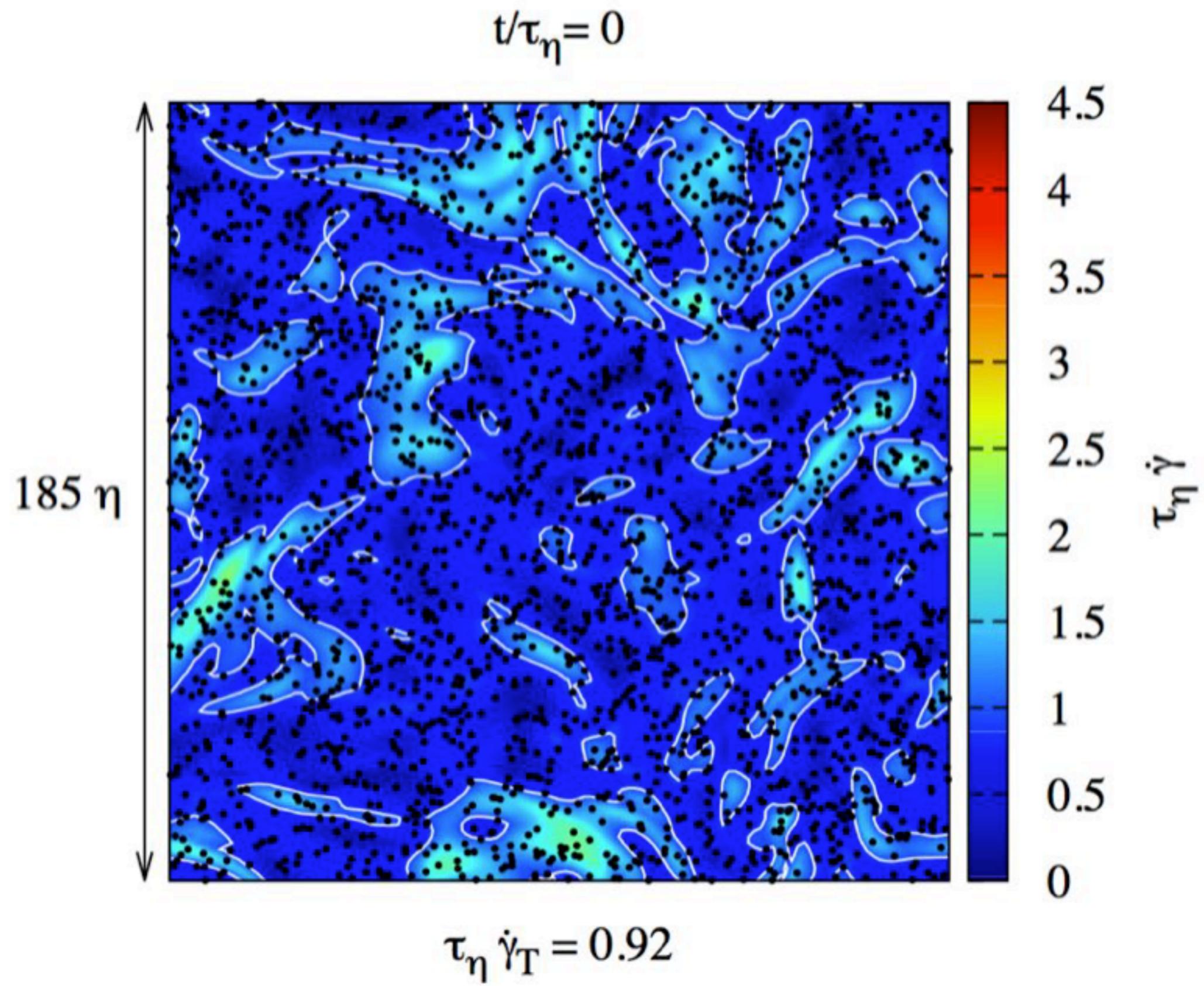
- Memory effect (explore delay - amplitude relation)
- Considering finite-size of domain of perception

**Test the model against real measurements in turbulence
(Needs new experimental data)**

Thank you!



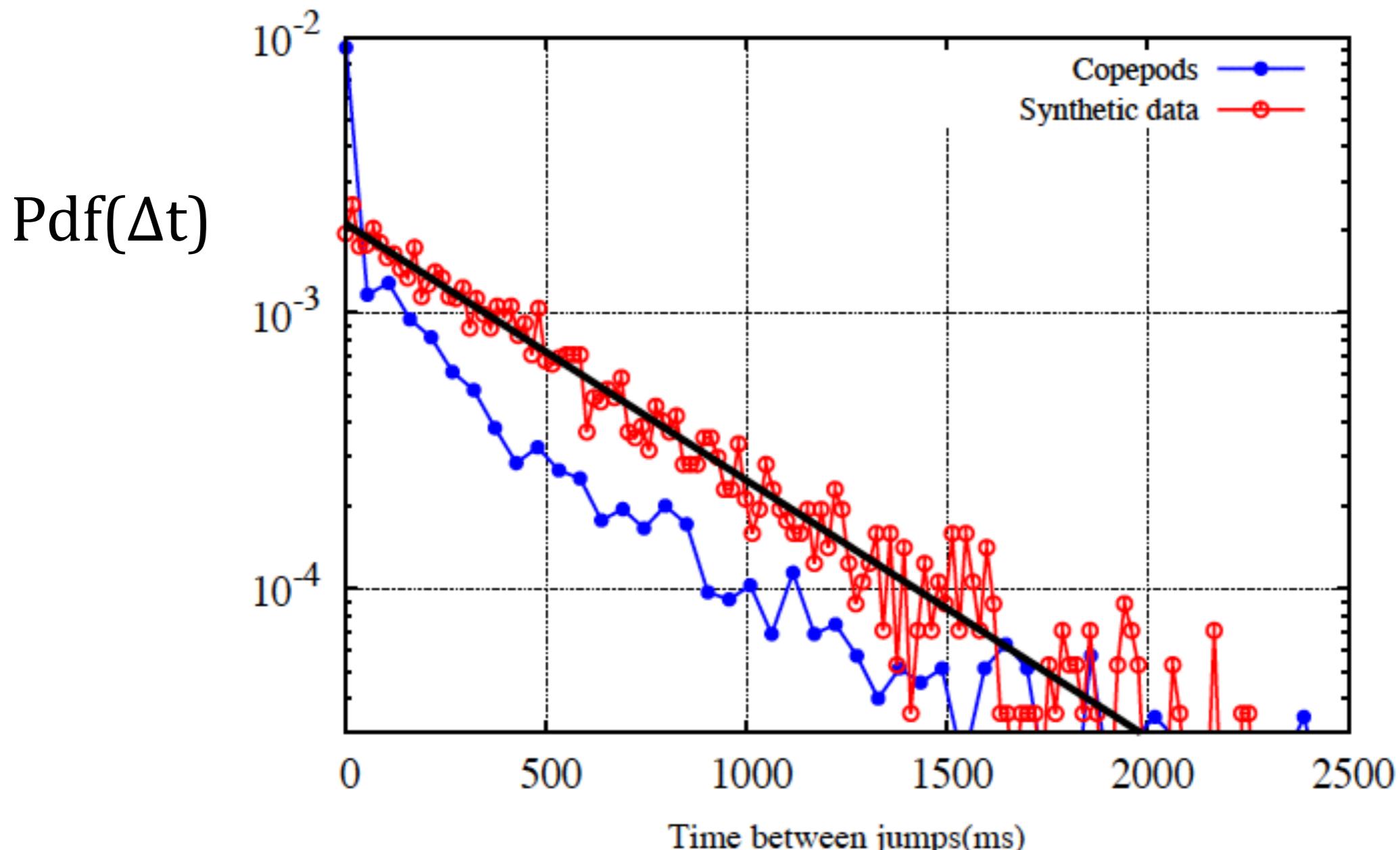
Thank you!





Back to data analysis

jump time-gap statistics



$$\Delta t = t_{\text{jump}}(n+1) - t_{\text{jump}}(n)$$



Back to data analysis

jump time-gap statistics

