

Motivations  
oooo

2D inert  
ooooo

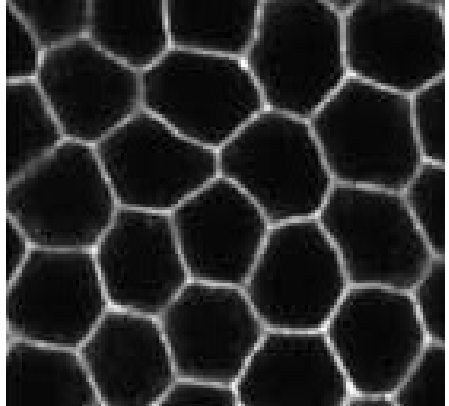
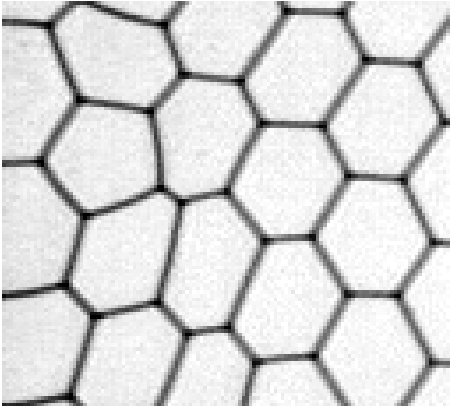
2D active  
oooooo

3D  
oo

Conclusion  
ooo

*foam - M. Asipauskas*

*tissue - Blankenship et al.*



# Disorder, elasticity, rearrangements

e.g. in foams or biological tissues

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# Outline

- 1 Motivations
- 2 2D inert
- 3 2D active
- 4 3D
- 5 Conclusion

Motivations

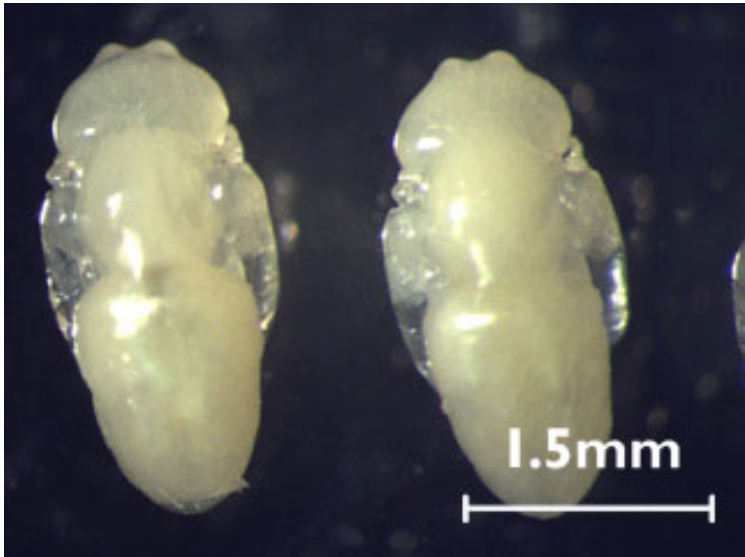
# Tissue morphogenesis

Multi-cellularity and neighbour changes



# Fruit fly metamorphosis

Larva → adult



*Drosophila*  
*melanogaster*  
pupae  
development

duration :  
5 days

# Multi-scale live imaging

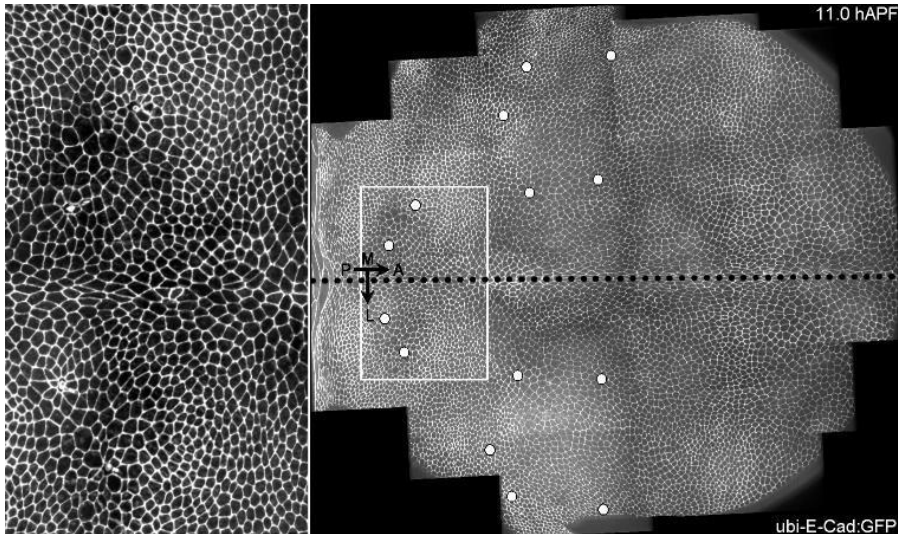
Bosveld

zoom

waist

dorsal thorax

neck



1 layer ~ 7000 cells

12-38h after pupa formation

~3 decades time & space

# Linking scales

cell  
scale



cell group  
scale



tissue  
scale

# Linking scales

cell  
scale



cell group  
scale



tissue  
scale

statistical physics :  
determine the  
material parameters

viscosity  $\eta$

stiffness  $G$

yield strain  $\epsilon_Y$

# Linking scales

cell  
scale



cell group  
scale



tissue  
scale

statistical physics :  
determine the  
material parameters

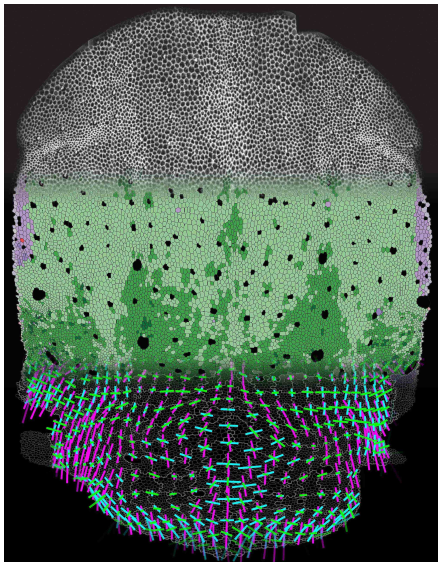
viscosity  $\eta$   
stiffness  $G$   
yield strain  $\epsilon_Y$

continuum mechanics :  
determine the  
dynamical fields

velocity  $V$   
strain  $\epsilon$   
stress  $\sigma$

# Continuous description

Guirao



It enables :

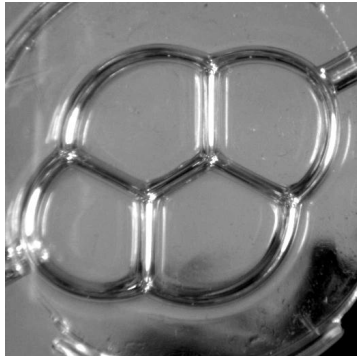
- compare experiments and/or simulations
- average them, determine their variability
- subtract them, determine effect of parameters

It requires :

- fluctuations average out
- cells in group : number  $\gg 1$
- thanks to average over space, time and samples

# Inert cellular materials

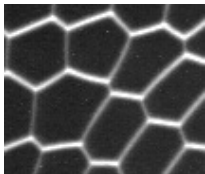
foam as model system



D. Cuvelier

# Deform a foam

Marmottant

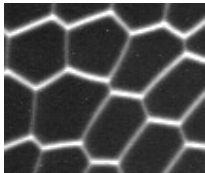


local energy minimum



# Deform a foam

Marmottant



local energy minimum

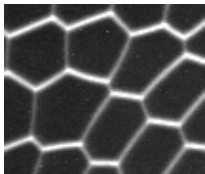
Small deformation

elastic solid

reversibly comes back  
to its initial shape

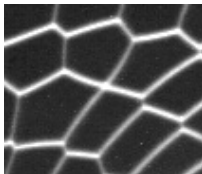
# Deform a foam

Marmottant



local energy minimum

yield  
 $\epsilon \gamma$   
→



neighbour change

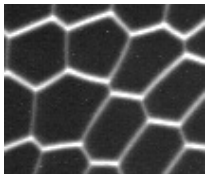
Small deformation

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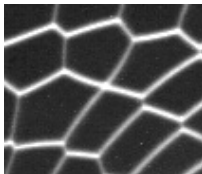
# Deform a foam

Marmottant



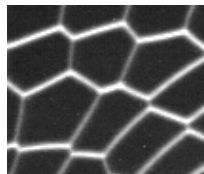
local energy minimum

yield  
 $\epsilon_Y$   
→



neighbour change

time  
 $\tau_R$   
→



relaxation to other minimum

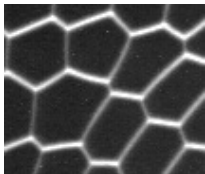
Small deformation

elastic solid

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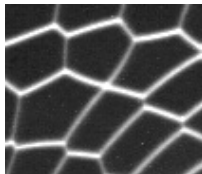
# Deform a foam

Marmottant



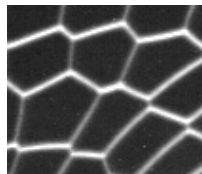
local energy minimum

yield  
 $\varepsilon_Y$   
→



neighbour change

time  
 $\tau_R$   
→



relaxation to other minimum

Small deformation

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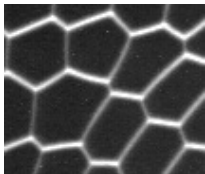
Large deformation

plastic solid

irreversibly sculpted,  
new shape

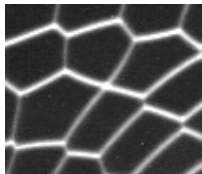
# Deform a foam

Marmottant



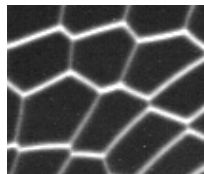
local energy minimum

yield  
 $\epsilon_Y$   
→



neighbour change

time  
 $\tau_R$   
→



relaxation to other minimum

Small deformation

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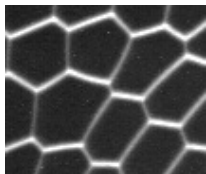
Quick deformation rate

viscous liquid

irreversibly flows,  
stress increases with rate

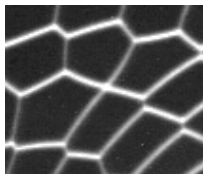
# Deform a foam

Marmottant



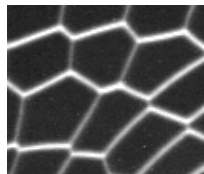
local energy minimum

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 $\tau_R$   
→



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Quick deformation rate

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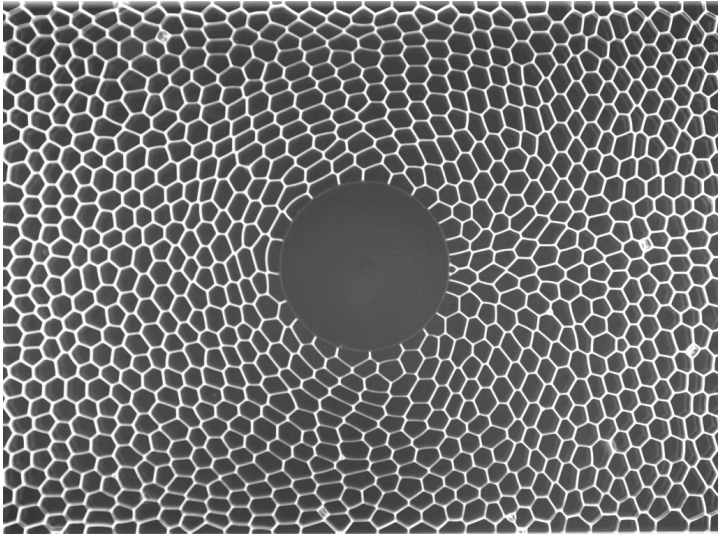
no gap, no overlap

→ deform through rearrangements  
→ viscous, elastic, plastic (VEP) behaviour

# Foam flow around obstacle

Dollet, Raufaste

- heterogeneous : variety of shears and elastic deformations
- can discriminate between models ?



control

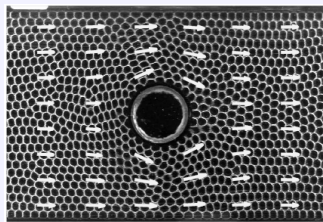
parameters :

- 2D
- water 1.2%
- monodisperse
- $V = 0.6$  cm/s

# Statistical measurements

Aubouy, Marmottant

## Velocity

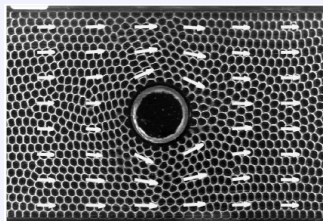




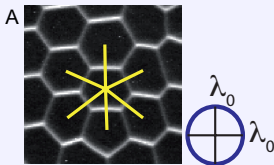
# Statistical measurements

Aubouy, Marmottant

## Velocity

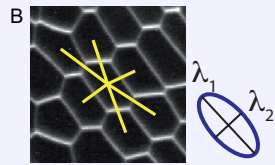


## Texture



isotropic  
circle

## Bubble shape and packing

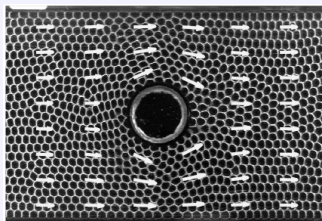


anisotropic  
ellipse

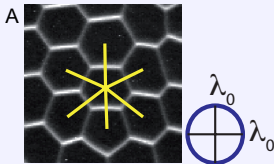
# Statistical measurements

Aubouy, Marmottant

## Velocity

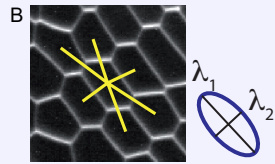


## Texture



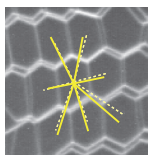
isotropic  
circle

## Bubble shape and packing



anisotropic  
ellipse

## Velocity gradient

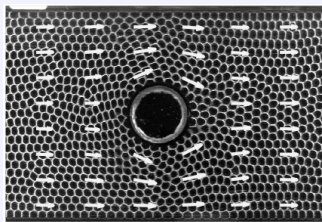


Shape change

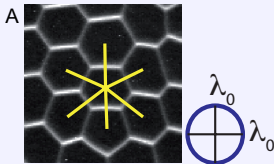
# Statistical measurements

Aubouy, Marmottant

## Velocity

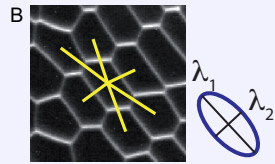


## Texture



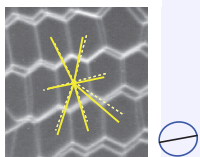
isotropic  
circle

## Bubble shape and packing



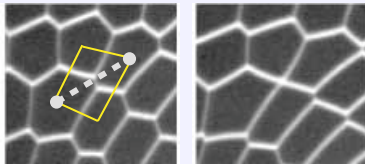
anisotropic  
ellipse

## Velocity gradient

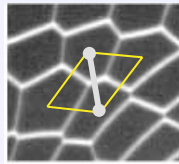


Shape change

## Plasticity



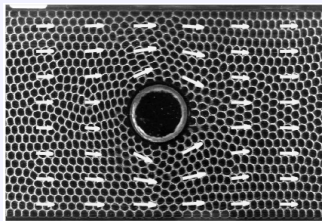
## Neighbour change



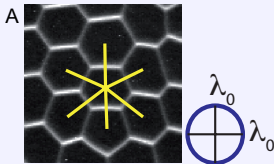
# Statistical measurements

Aubouy, Marmottant

## Velocity

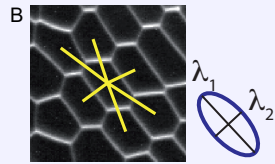


## Texture



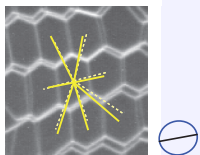
isotropic  
circle

## Bubble shape and packing



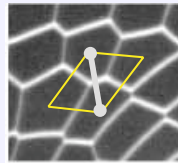
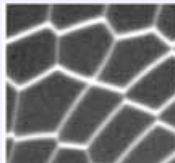
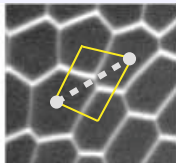
anisotropic  
ellipse

## Velocity gradient



Shape change

## Plasticity



## Neighbour change

deformation rates : total = elastic + plastic

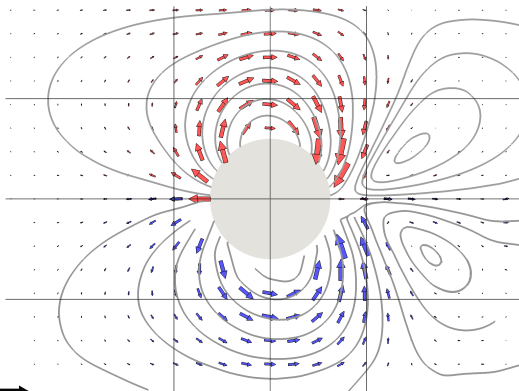
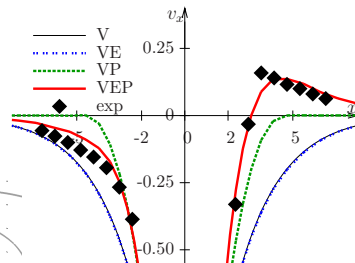
# Prediction ?

Cheddadi

speed along the main axis  $y = 0$   
referential moving with the foam

visco-elasto-plastic model  
main parameter : yield strain

prediction : continuous model



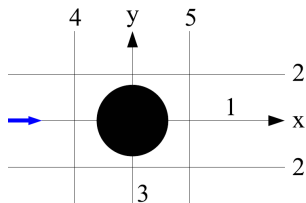
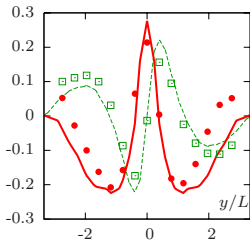
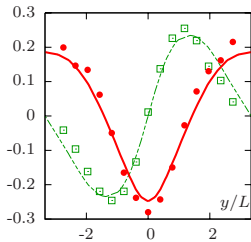
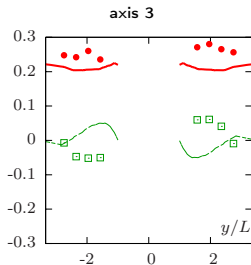
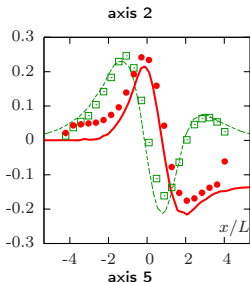
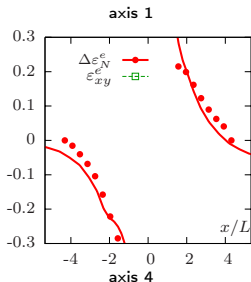
→ dry foam experiment : discrete measurements

Good agreement

- amplitude of  $v$
- orientation of  $v$
- recirculation zones
- up/down asymmetry
- $v = 0$  point
- overshoot

# Graphs of elastic strain tensor

$xx - yy$  and  $xy$  components



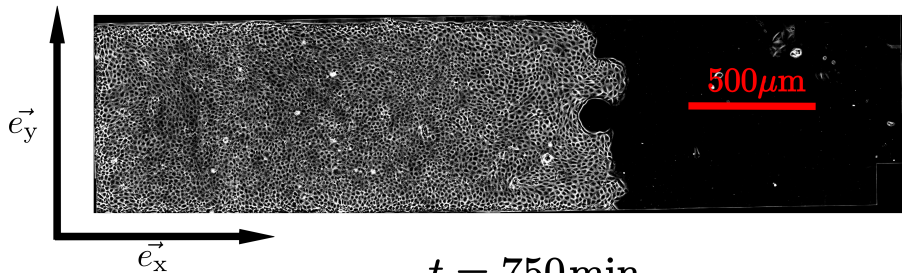
Agrees on **position** and **amplitude** of local extrema

# Cell monolayer around an obstacle

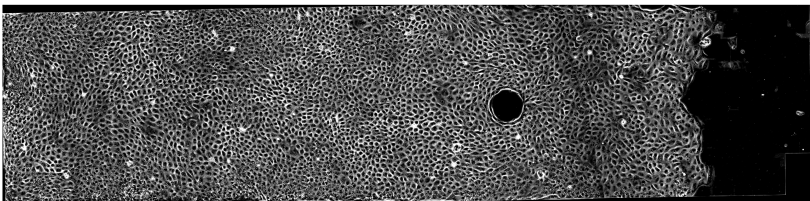
# Migration around an obstacle

Tlili

$t = 0 \text{ min}$



$t = 750 \text{ min}$

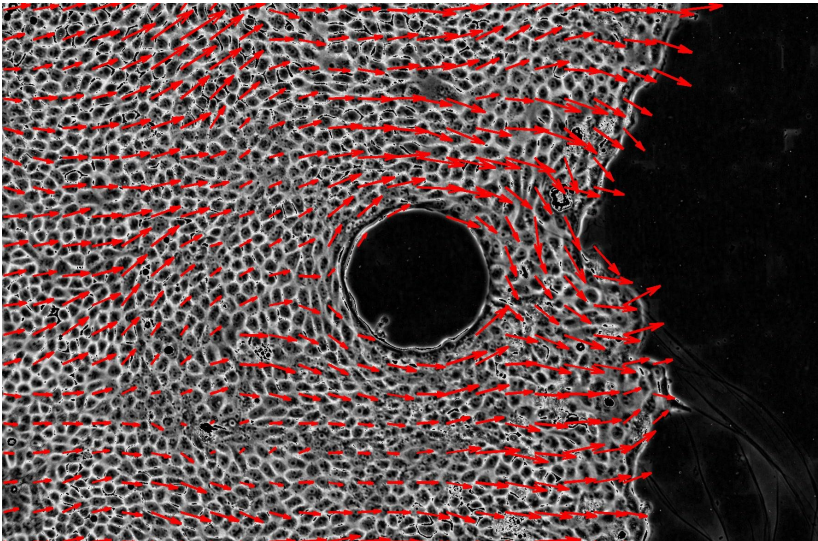




# Velocity field

Tlili

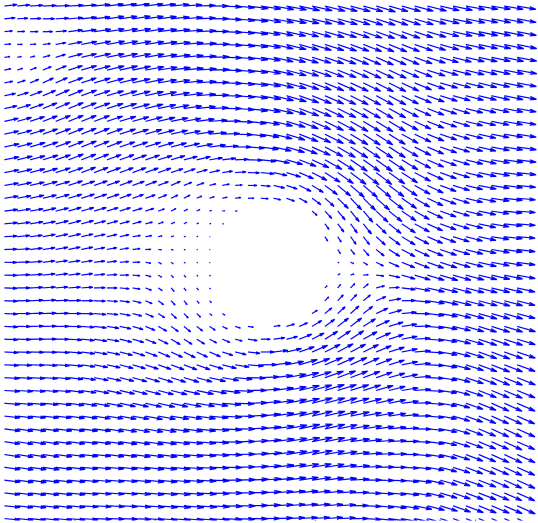
image correlation : "particle image velocimetry"  
no need to identify ("segment") cell contours



# Averaged velocity field

Tlili, Durande

$2\mu\text{m}/\text{min}$   
→

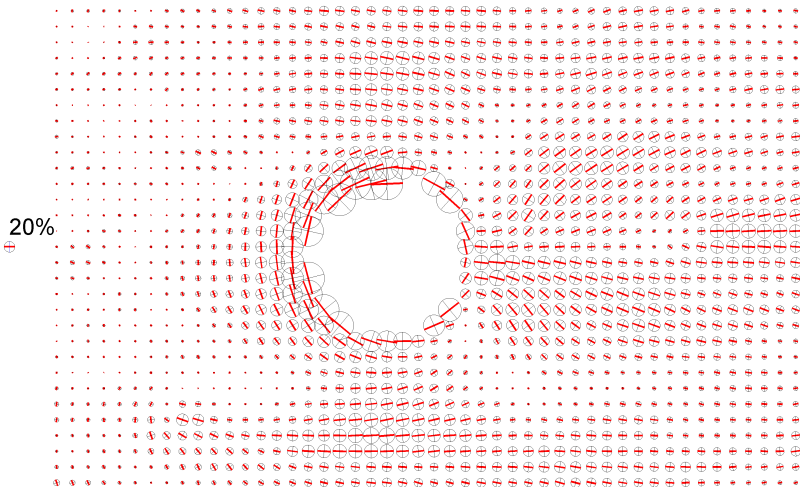


average  
over time  
and/or over  
experiments

# Deformation field

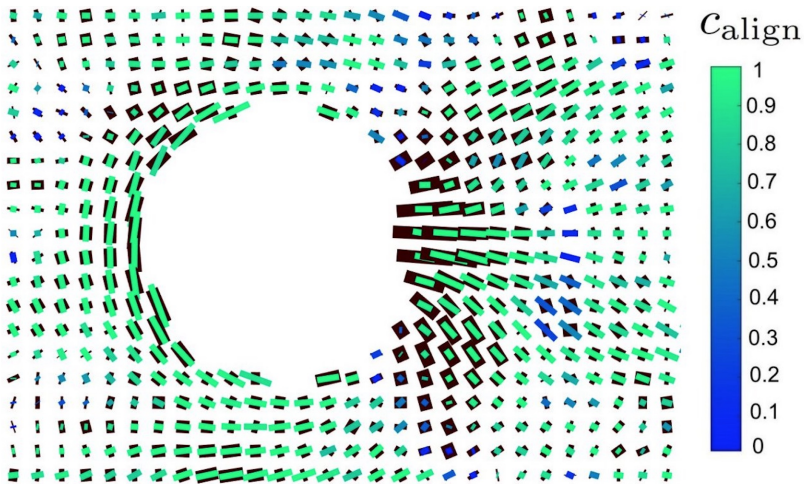
Tlili, Durande

cell shape : "Fourier transform"  
no need to identify ("segment") cell contours



# Comparison

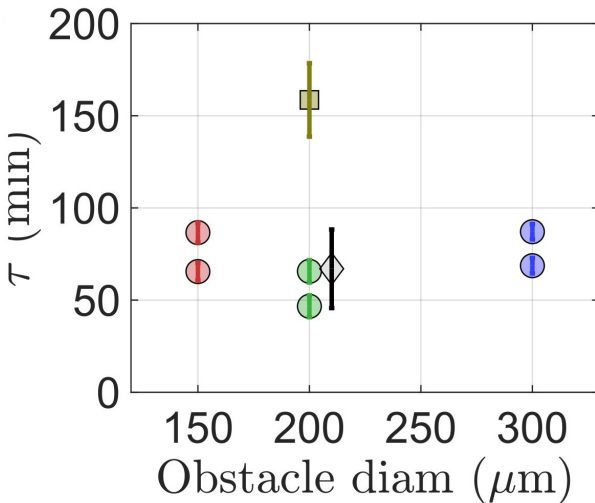
Cell rearrangements & cell deformation fields



visco-elastic liquid behaviour

visco-elastic time 70 min

# Visco-elastic time

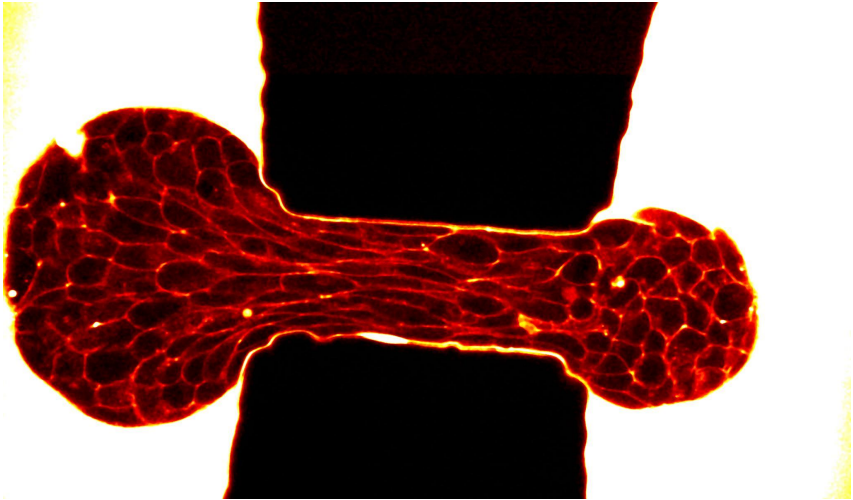


$\tau$  independent on obstacle size & independent on division rate  
slowed down by myosin inhibitor, related to cell rearrangements

# Cell aggregate

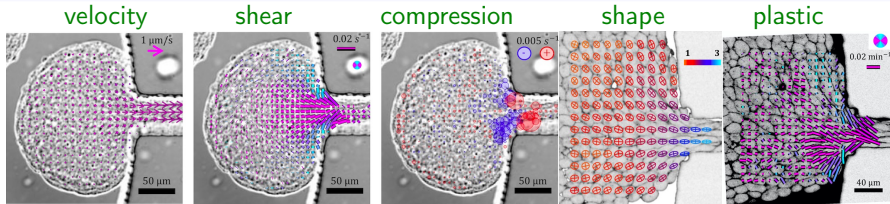
## through a constriction

# Aspire a cell aggregate

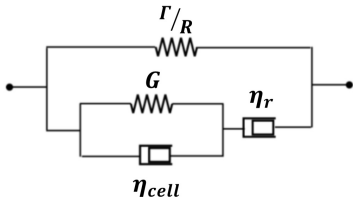


- 1 movie = 3 experiments : **constriction, divergence, elasto-capillarity**
- heterogeneous : **induced cell rearrangements, many informations**
- measure and link : **cell shape, neighbour changes, local viscoelastic properties**

# All measures without segmentation



cell group scale visco-elastic relaxation time	$\tau_r$	$10^3$ s
cell group scale viscosity	$\eta_r$	$10^5$ Pa.s
elastic modulus	$G$	$10^2$ Pa
cell scale visco-elastic relaxation time	$\tau_{cell}$	$10^2$ s
cell scale viscosity	$\eta_{cell}$	$10^4$ Pa.s
aggregate scale capillary modulus	$(\Gamma/R)$	$10^2$ Pa



$\eta_r$  from previous experiments

Elasto-capillar number  $\sim 1$



# Conclusion

# Summary of approach

## Objects with disorder, elasticity, rearrangements

- Very **general** applications : bubbles in foam, cells in tissue, grains in polycrystal, atoms in glass, drops in emulsion, magnetic domains, packed soft objects, etc
- total deformation rate  
= **elastic** deformation rate  
+ **plastic** deformation rate
- experiments and simulations which **vary** in space
- **coarse grain** → continuous description
- **compare** experiments and/or simulations

# Summary of results

How do objects with **disorder, elasticity** flow?

- **powerful** statistical tools to analyse data
- cellular structure → emergent **solid** behaviour
- inert case → coarse-grain & model **predicts** flow
- activity → emergent **collective** migration
- extract **rheological** equations and parameters

# Perspectives

in progress

## Model

Shourick

Résumé : On pose  $\sigma^i = \sigma_{ij}^i$ ,  $d^i = j_{ij}^i$  et  $\rho = 0$ .

$$\frac{\partial \rho}{\partial t} + \nabla \cdot (j \rho) = 0, \quad (1.65a)$$

$$-\nabla \cdot (j \sigma) + \sigma_{ij}^{(ij)} (x_i = 0) = 0, \quad (1.65b)$$

$$\sigma = 2(1 - \lambda)(\nabla v^i + (\nabla \cdot v) \delta + \omega_j R_{ij}) + \lambda(\sigma^i - \sigma^i \delta) - \gamma \rho_i j, \quad (1.65c)$$

$$W \frac{\partial \sigma^i}{\partial t} + (1 + \lambda' W v) \sigma^i = 2D(v) - \lambda' v \cdot \sigma, \quad (1.65d)$$

$$W \left[ \frac{D \sigma^i}{Dt} + 2(\nabla \cdot v) \sigma^i \right] + (1 + \lambda' W v) \sigma^i = -2\nabla \cdot v - \lambda' v, \quad (1.65e)$$

$$\frac{d j_{ij}}{dt} = 2v_{ij}, \quad (1.65f)$$

$$\frac{d \sigma}{dt} = j \cdot \omega^i + \sigma(\nabla \cdot v) d^i + \frac{2\rho}{L} j, \quad \nabla(\nabla \cdot v) = 2\sigma d, \quad (1.65g)$$

$$-\gamma \frac{\rho_i}{\eta L^2} \Delta v - \gamma \frac{\rho_i}{\eta L^2} \nabla v \cdot \nabla v = \text{tr } \sigma - \tau, \quad (1.65h)$$

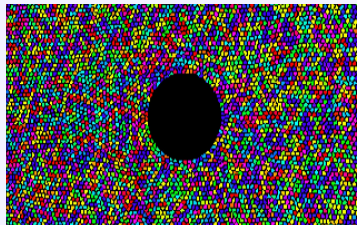
$$\tau = \text{tr } \sigma = (1 - \lambda) \left[ 1 - \gamma \frac{3\lambda'}{2} - \gamma \frac{\lambda' W v}{2} (\text{tr } \sigma^i + \sigma^i) \right] \rho - (1 - \lambda) \frac{\gamma}{2} (\text{tr } \sigma^i + \sigma^i) - \gamma \rho_i \text{tr } j, \quad (1.65i)$$

$$-\gamma \frac{\rho_i}{\eta L^2} \rho \Delta \omega - \gamma \frac{\rho_i}{\eta L^2} \nabla \omega \cdot \nabla \rho + 4(1 - \lambda) \rho \omega = - (1 - \lambda) \rho^2 R_{ij} - \nabla(\nabla \cdot v), \quad (1.65j)$$

$$-\gamma \frac{\rho_i}{\eta L^2} \rho \Delta \omega_i - \gamma \frac{\rho_i}{\eta L^2} \nabla \rho \cdot \nabla \omega_i = -\rho R_{ij} \cdot \sigma, \quad (1.65k)$$

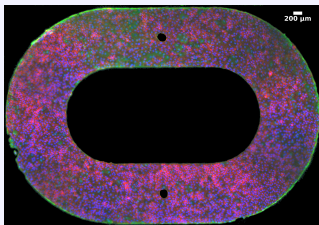
## Simulations

Beatrice



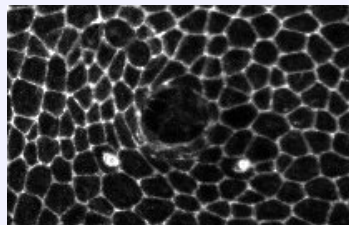
## Boundaries

Durande



## In vivo

Villedieu



# Thanks

- **MSC - biophysics**

- **MSC - theory**

- **Lyon - biophysics**

- **Grenoble - foams**

- **Grenoble - maths**

- **Curie - fly genetics**

- **Curie - physics**

- **Heidelberg - mouse**

- **Monod - fly evolution**

- **Japan - force inference**

- **Brazil - simulations**

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