Frustration and fluctuations in tissue growth

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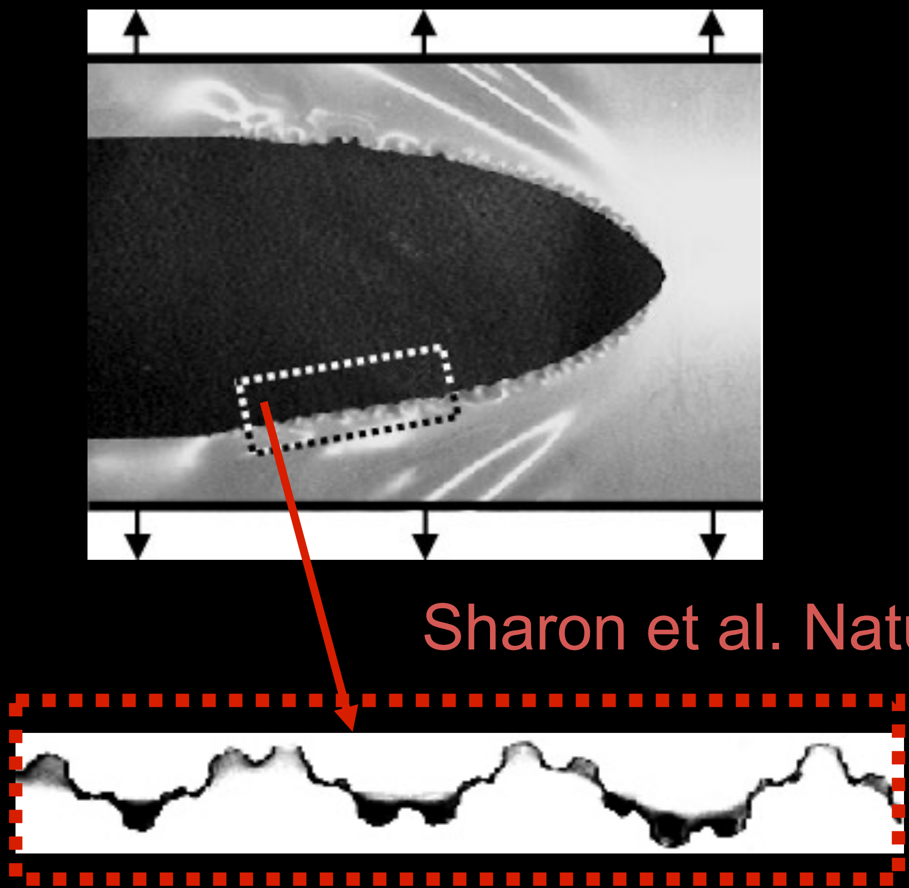
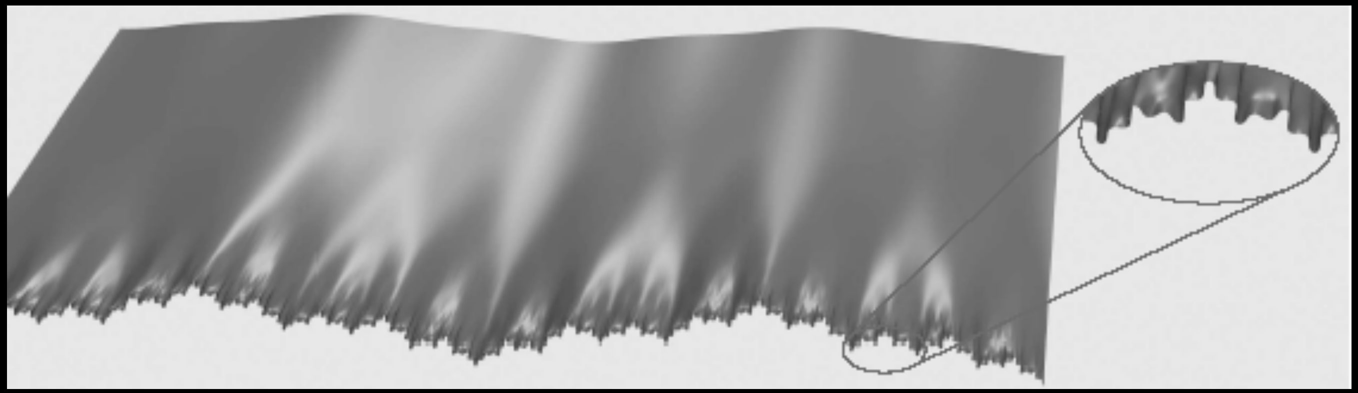
How do organs and organisms reach well-defined size and shape?

Focus on thin organs

Expanding thin elastic sheets: experiments and theory



Sharon et al. Nature 2002



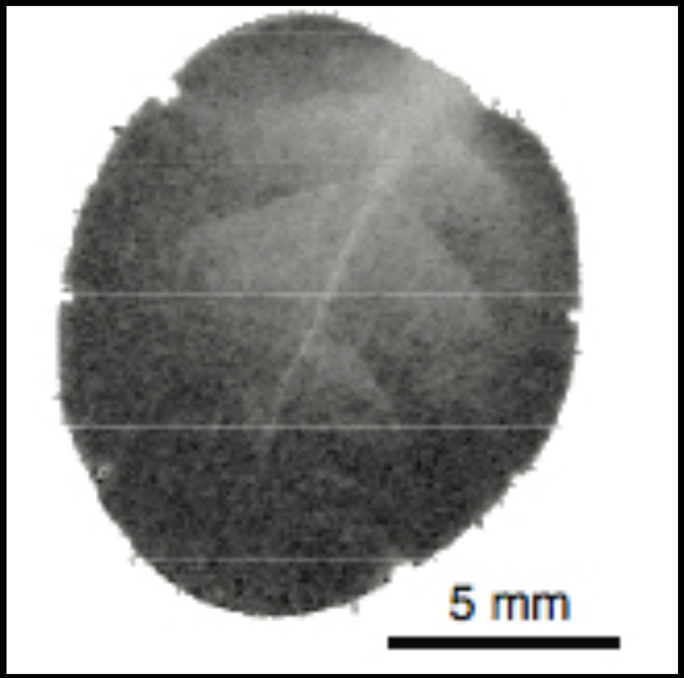
Audoly and Boudaoud PRL 2003

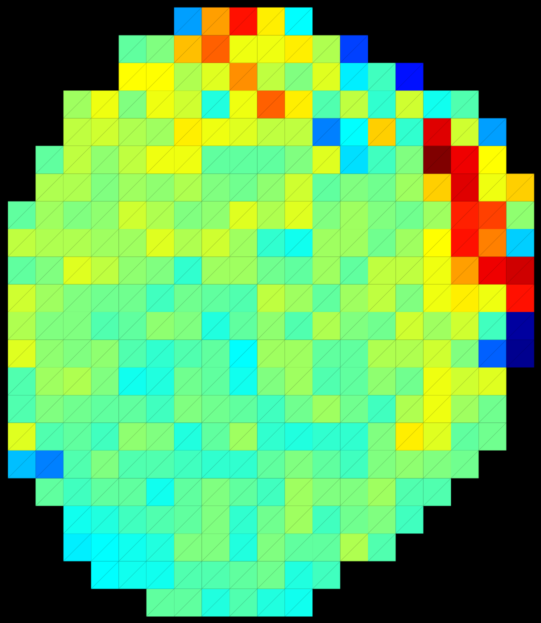
Inhomogeneously growing thin sheets buckle by default


JM Allain

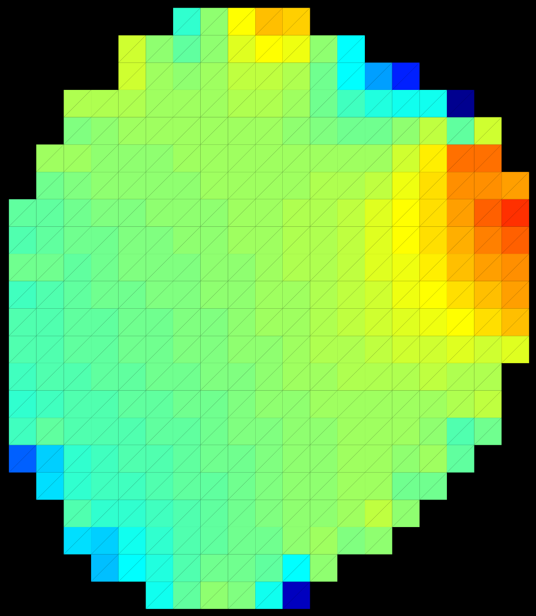
How do leaves achieve flatness?

Does flatness constrain growth?





Growth
1/A.dA/dt



Growth from contour
and conformal map

Alim et al. Phys Biol 2016
Similar results: G. Mitchison, JTB 2016

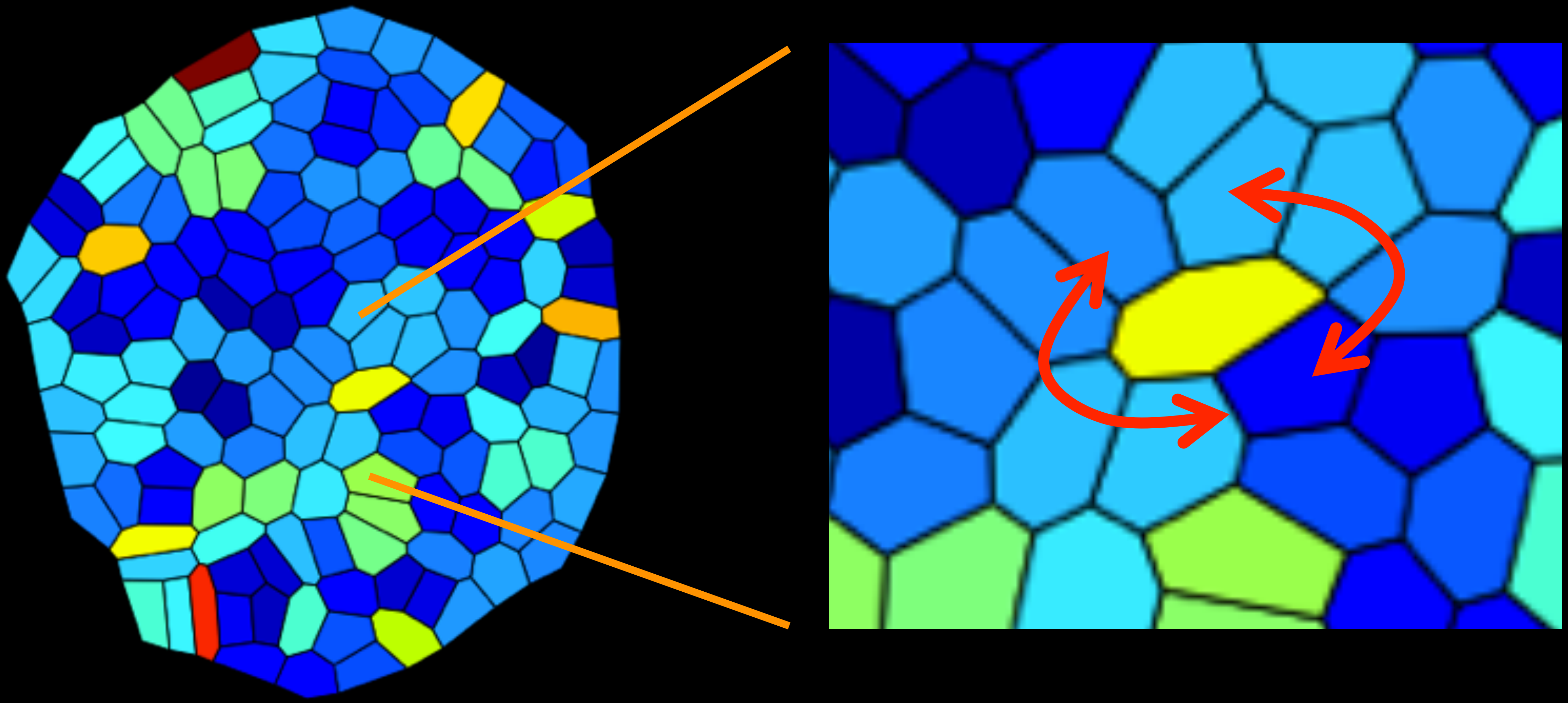
Conformal maps retrieve
2D isotropic growth

But local fluctuations

What is the impact of local fluctuations on overall shape of a flat organ?

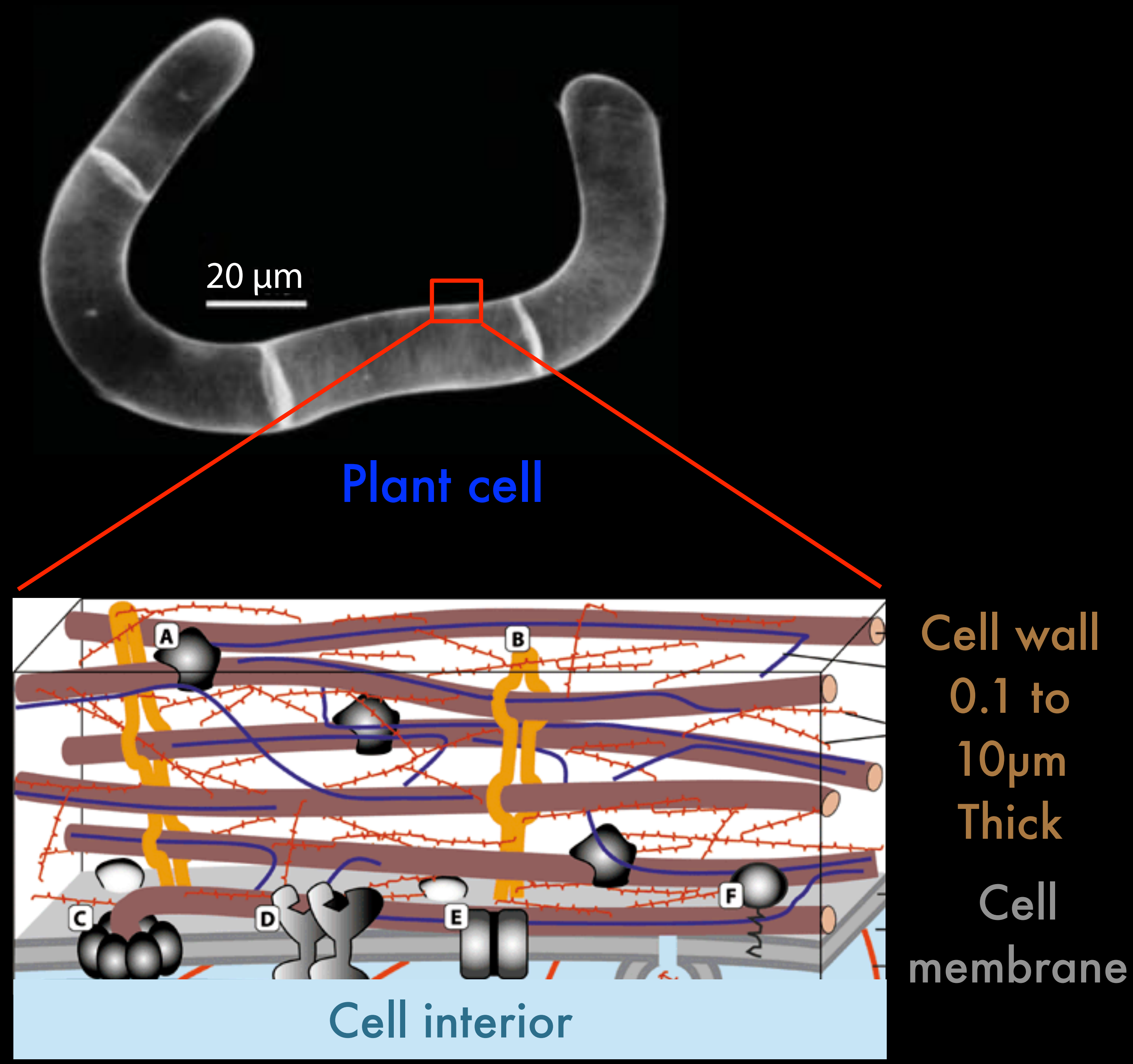
Antoine Fruleux

Heterogeneous growth and frustration



Circumferential mechanical stress around fast growing cells

Do plant cells react?



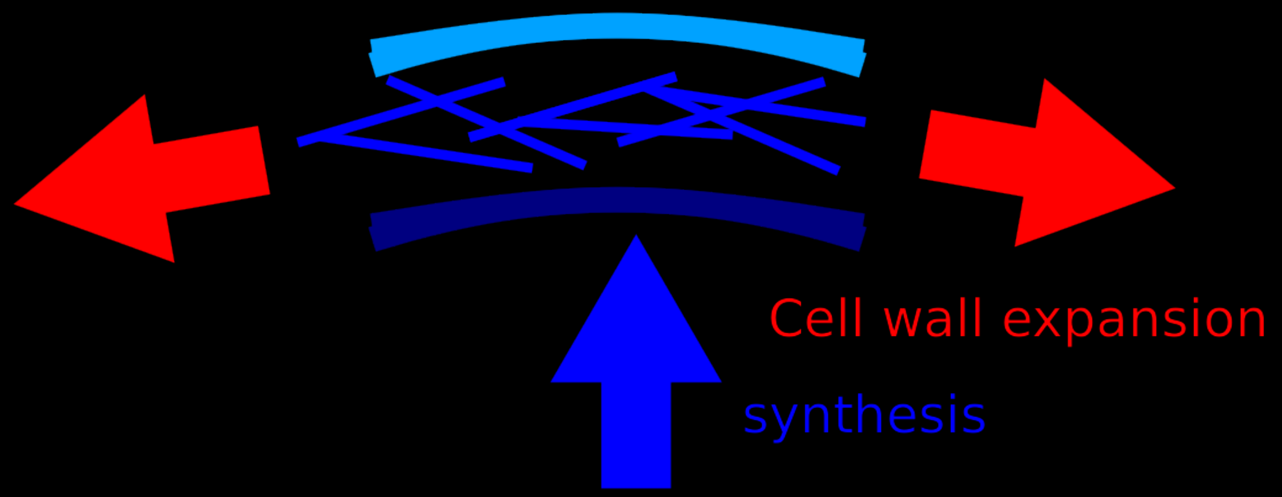
Plant cells react: Cellulose is deposited in the direction of maximal mechanical stress

What is the effect of such mechanical feedback on organ shape?

Antoine Fruleux
ENS Lyon

A stochastic viscous model for cell wall expansion

- Viscous cell wall on long time scales
- Tension due to cell pressure
- Increase in synthesis when tension is increased (density and orientation of fibres)
- Fluctuations in synthesis



wall tension

$$\overline{\sigma}(\overline{\dot{\gamma}}, \rho, \overline{s})$$

strain rate tensor

$$\overline{\dot{\gamma}} = (\partial_{\vec{r}}\vec{v}) + (\partial_{\vec{r}}\vec{v})^T$$

→ $\vec{v}$ flow velocity

$$\overline{\omega} = (\partial_{\vec{r}}\vec{v}) - (\partial_{\vec{r}}\vec{v})^T$$

$$\partial_{\vec{r}} \cdot \left[\overline{\sigma} - \overline{1}P\right] = \vec{0}$$

wall components:

→ ρ density

$$\partial_t \rho + \partial_{\vec{r}} \cdot \{\rho\, \vec{v}\} = \kappa_\rho$$

convection + synthesis

→ $\overline{s}$ anisotropy

$$\partial_t \overline{s} + (\vec{v} \cdot \partial_{\vec{r}})\overline{s} + \overline{\omega} \cdot \overline{s} - \overline{s} \cdot \overline{\omega} = \overline{\kappa}_s$$

advection+ corotation+ synthesis

$$\kappa_\rho = \langle \kappa_\rho \rangle - \frac{1}{\tau_\rho} \left(\Delta\rho - \beta_\rho \Delta\sigma \right)$$

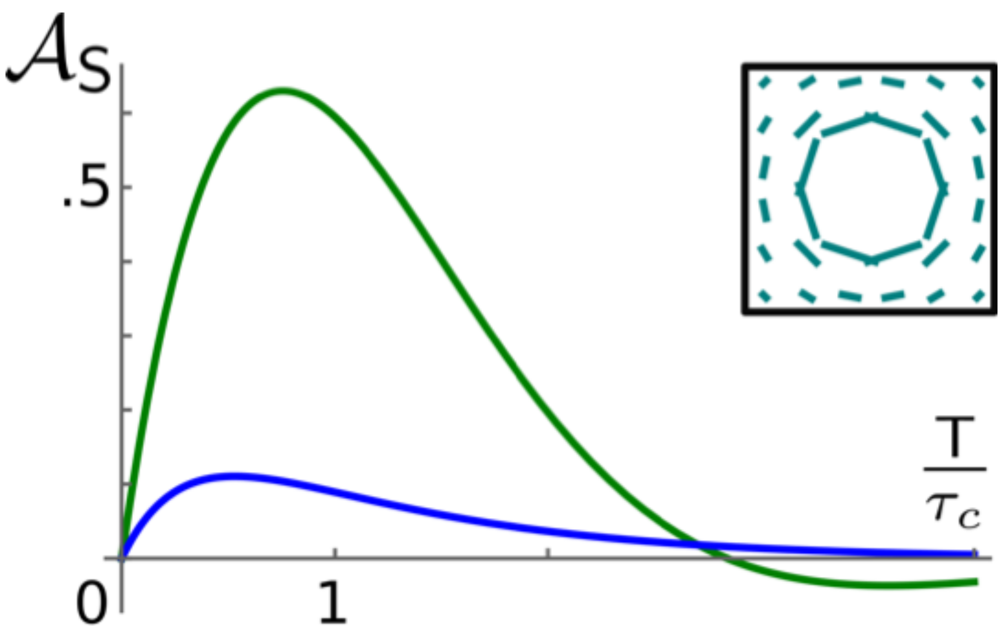
$$\overline{\kappa}_s = -\frac{1}{\tau_s} \left(\overline{s} - \beta_s \overline{\sigma}_a \right)$$

Generic model Similar to models for animal tissues, with feedback in addition

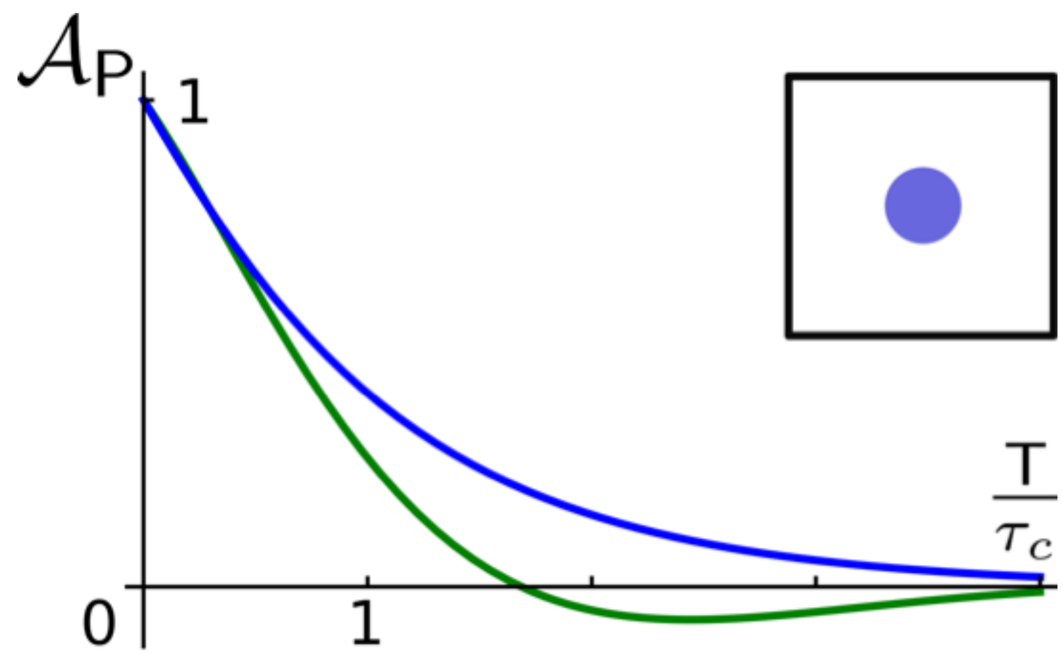
Response to local reduction in synthesis

Low anisotropic mechanical feedback

High anisotropic mechanical feedback



Tissue anisotropy



Tissue density

wall tension

$$\overline{\sigma}(\dot{\overline{\gamma}}, \rho, \overline{s})$$

strain rate tensor

$$\dot{\overline{\gamma}} = (\partial_{\vec{r}}\vec{v}) + (\partial_{\vec{r}}\vec{v})^T$$

→ $\vec{v}$ flow velocity

$$\overline{\omega} = (\partial_{\vec{r}}\vec{v}) - (\partial_{\vec{r}}\vec{v})^T$$

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wall components:

→ ρ density

$$\partial_t \rho + \partial_{\vec{r}} \cdot \{\rho\,\vec{v}\} = \kappa_\rho$$

convection + synthesis

→ $\overline{s}$ anisotropy

$$\partial_t \overline{s} + (\vec{v} \cdot \partial_{\vec{r}})\overline{s} + \overline{\omega} \cdot \overline{s} - \overline{s} \cdot \overline{\omega} = \overline{\kappa}_s$$

advection+ corotation+ synthesis

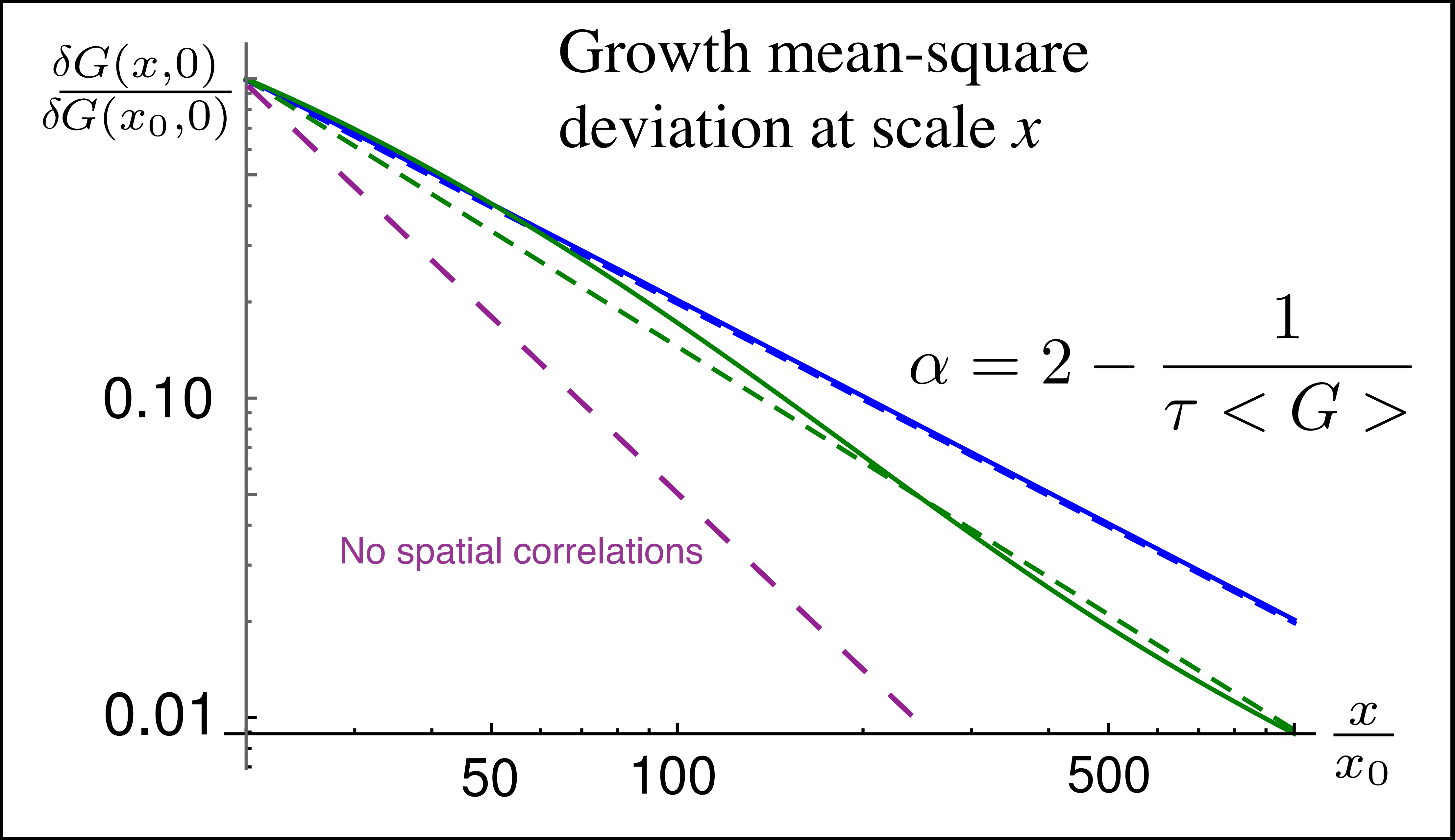
$$\kappa_\rho = \langle \kappa_\rho \rangle - \frac{1}{\tau_\rho}\left(\Delta\rho - \beta_\rho \Delta\sigma \right) + \Delta\kappa_\rho$$

$$\overline{\kappa}_s = -\frac{1}{\tau_s}\left(\overline{s} - \beta_s \overline{\sigma}_a \right) + \Delta\overline{\kappa}_s$$

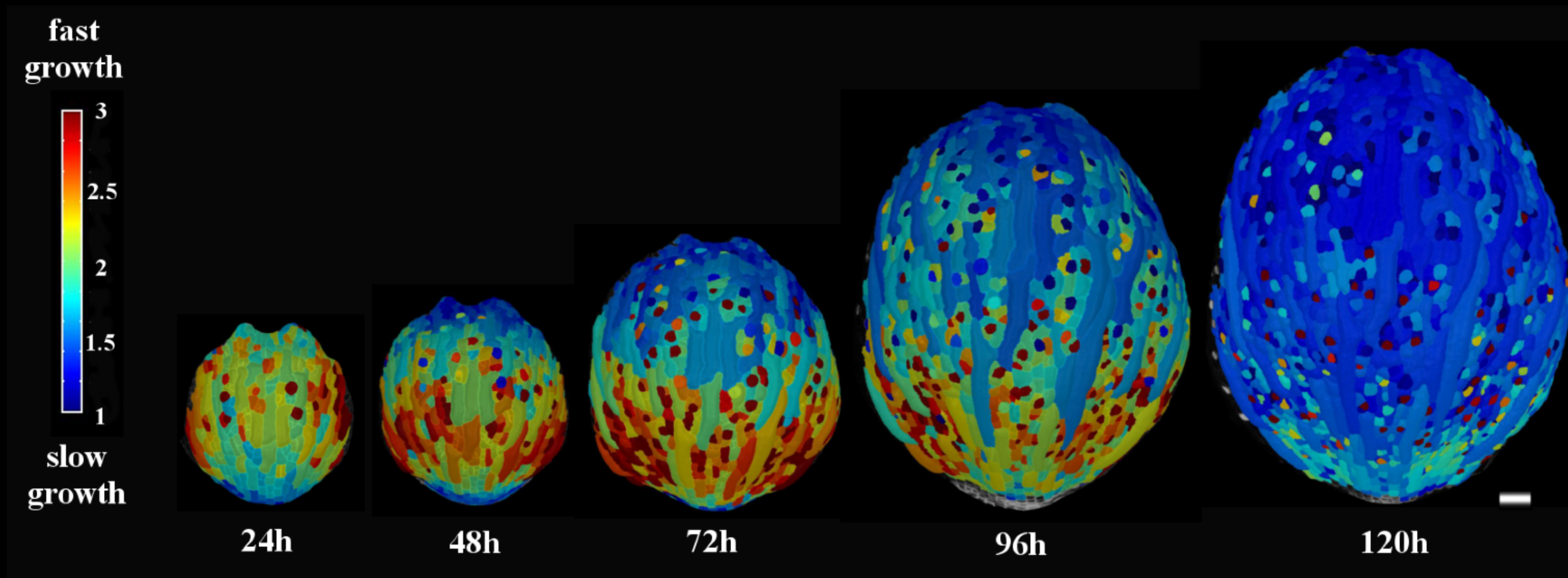
$$\langle \Delta\kappa_\rho(\vec{r},t)\Delta\kappa_\rho(\vec{r}',t')\rangle = K\, g\left(\frac{|\vec{r}-\vec{r}'|}{\xi_0}\right)\delta(t-t')$$

$$\langle \Delta\kappa_s(\vec{r},t)\Delta\kappa_s(\vec{r}',t')\rangle = S\, g\left(\frac{|\vec{r}-\vec{r}'|}{\xi_0}\right)\delta(t-t')$$

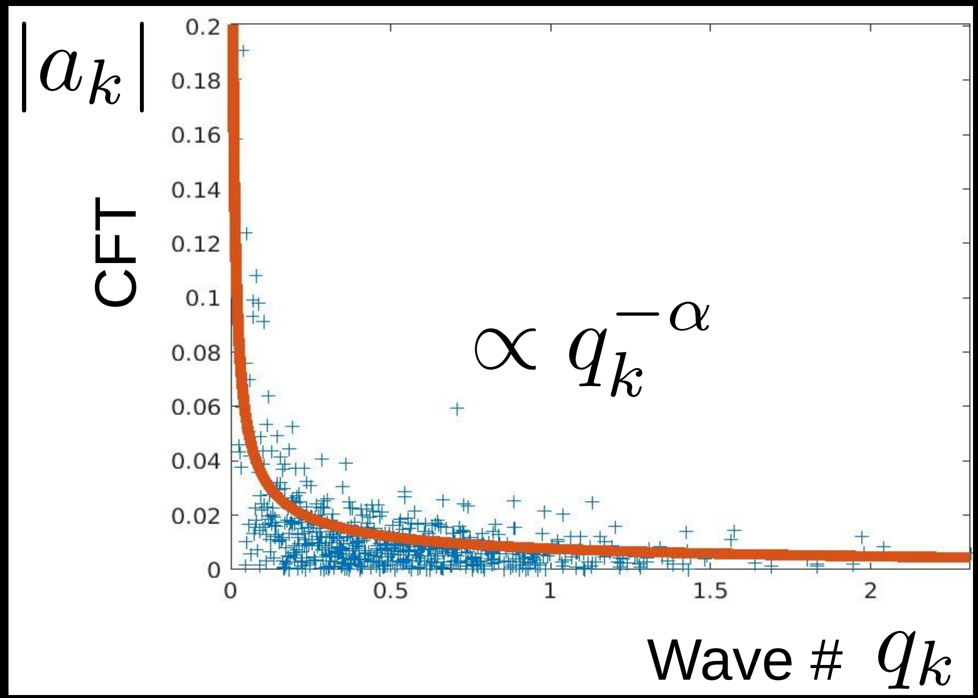
Growth fluctuations

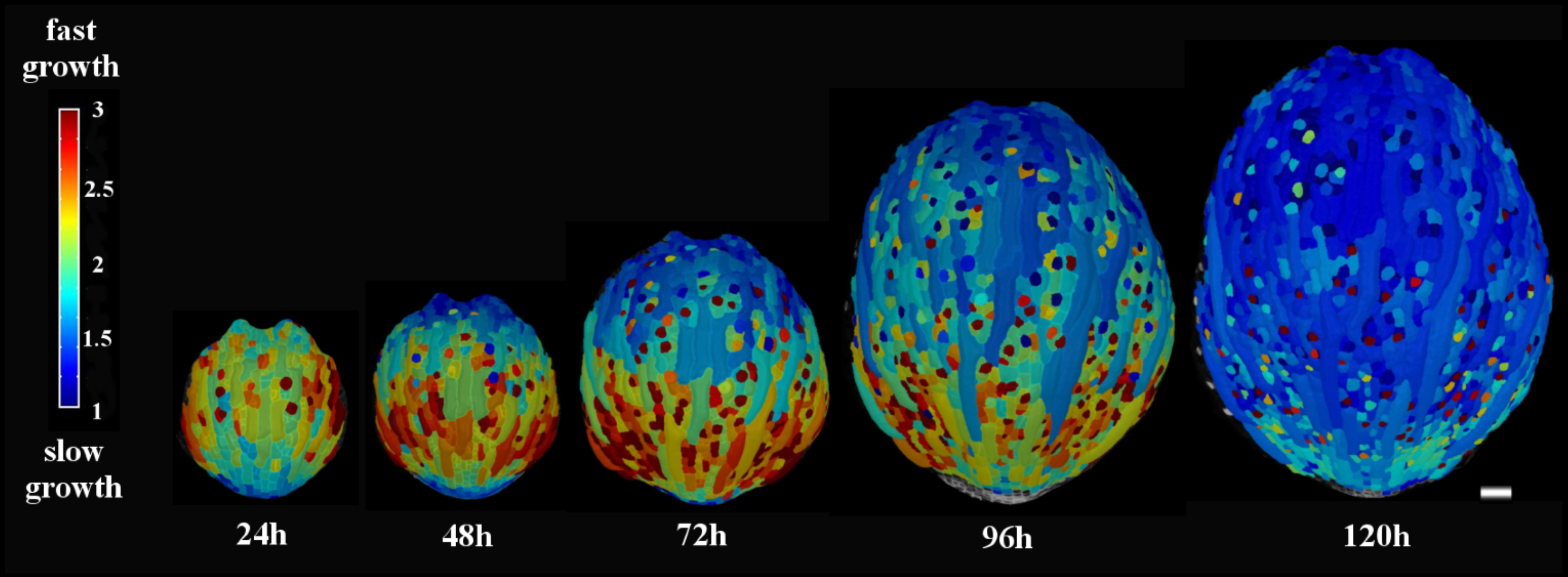


Long-range
correlations

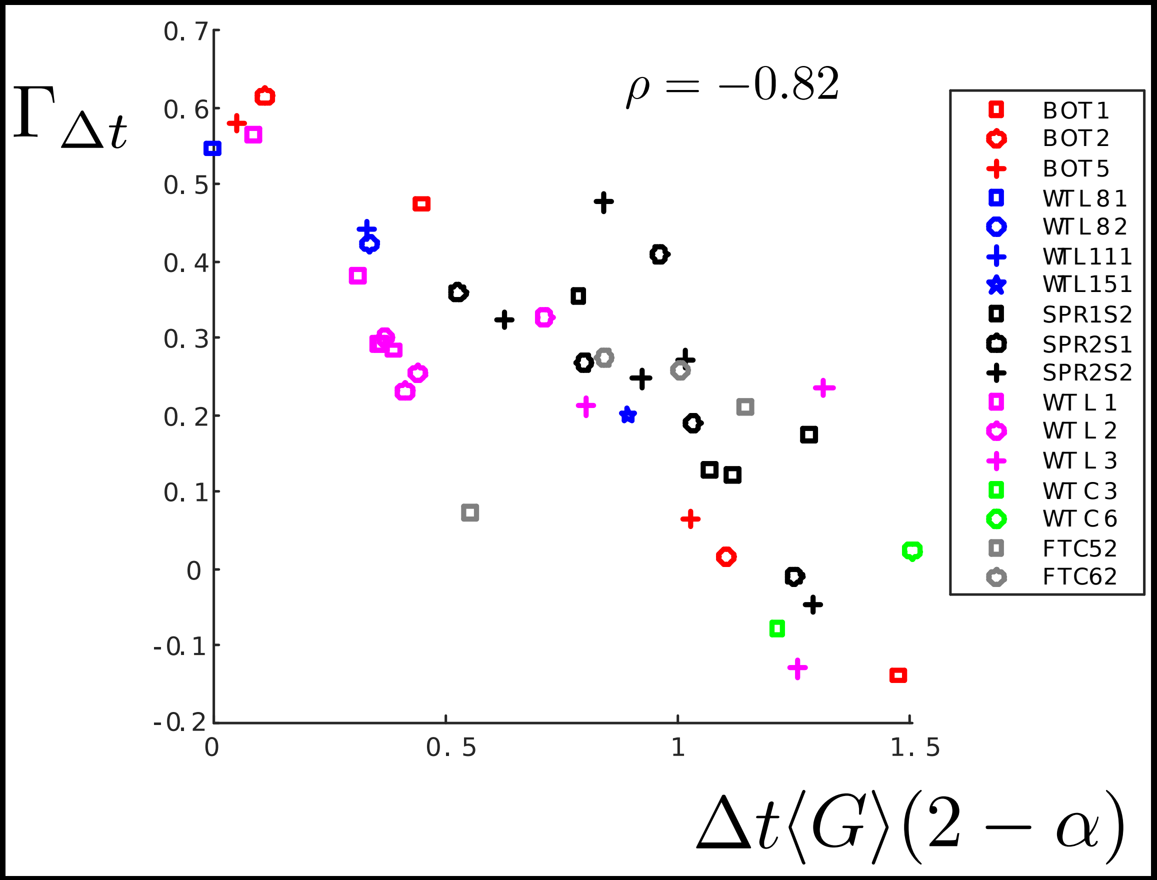


- Live imaging of growing flowers
- Quantification of rate of increase in area
- New spectral decomposition method

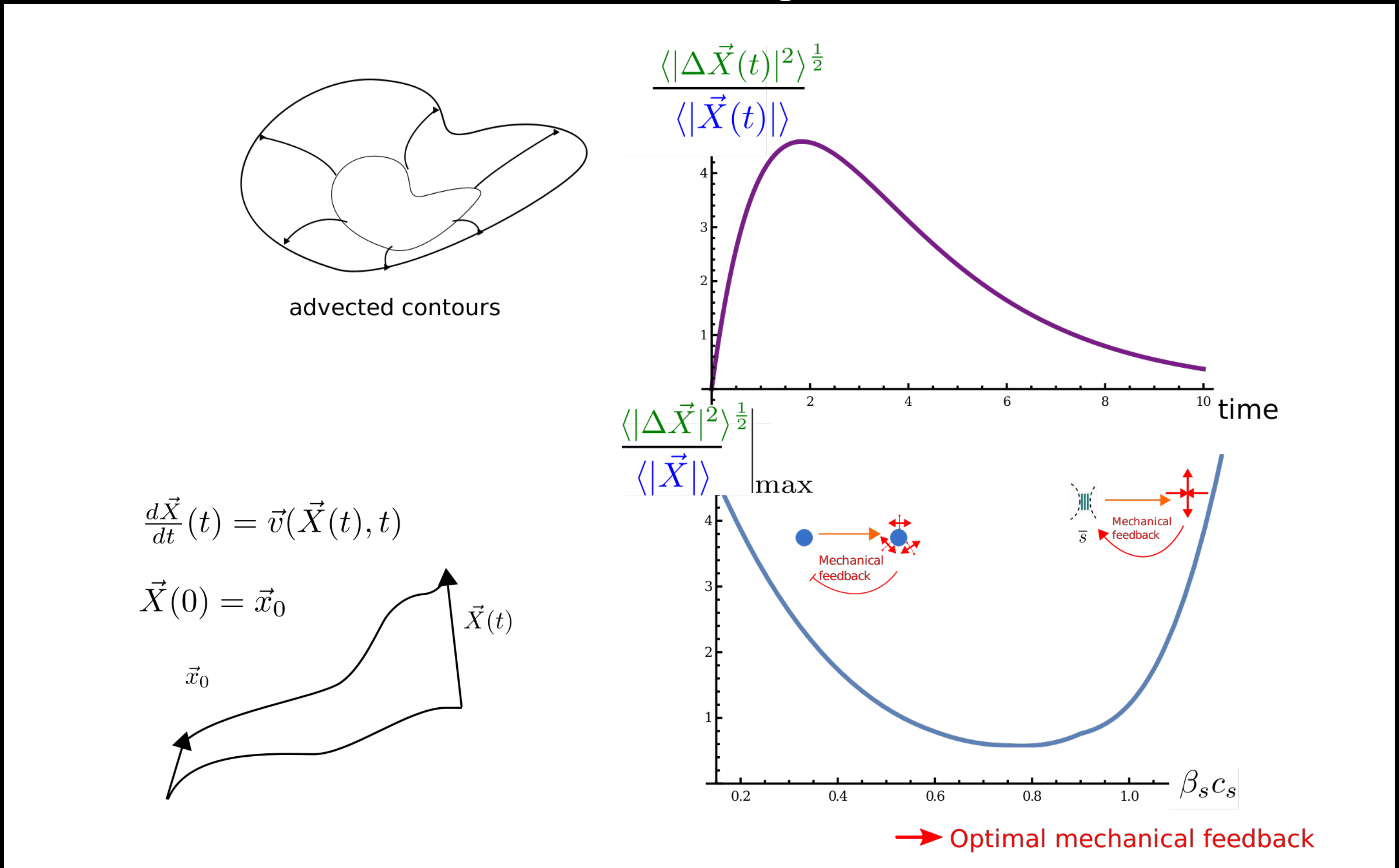




- Temporal correlations vs. time delay / theoretical correlation time



Fluctuations of organ contours



To be tested in experiments

Conclusions

- Long-range correlations in growing tissue

- Range modulated by mechanical feedback

- An optimum of response to mechanical stress may ensure a minimal variability in shape

Fruleux & Boudaoud, PNAS (2019);
Phys Rev Res (2021);
in progress (2021).

Open questions

- Is mechanical feedback always ‘stabilising’?
- How does this framework extend to 3D tissues?
- Do fluctuations enable living systems to sense their state?
- Are fluctuations important for size determination?