Quantifying active and resistive stresses in adherent cells.

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To understand cell migration, it is crucial to gain knowledge on how cells exert and integrate forces on/from their environment. A quantity of prime interest for biophysicists interested in cell movements modeling is the intracellular stresses. Up to now, three different methods have been proposed to calculate it, they are all in the regime of the thin plate approximation. Two are based on solving the mechanical equilibrium equation inside the cell material (Monolayer Stress Microscopy, and Bayesian Inference Stress Microscopy) and one is based on the continuity of displacement at the cell/substrate interface (Intracellular Stress Microscopy). We show here using 3D FEM modeling that these techniques do not calculate the same quantities (as was previously assumed), the first techniques calculate the sum of the active and resistive stresses within the cell, whereas the last one only calculate the resistive component. Combining these techniques should in principle permit to get access to the active stress alone.

Keywords: biological physics, mechanobiology, traction force microscopy, intracellular stress microscopy, elasticity

I. INTRODUCTION

Cell motility is at the core of both many physiological processes (such as embryogenesis, wound healing...) and pathological processes such as metastasis in cancer $^{[1,2]}$. In order to move, cells need to exert forces on its environment $^{[3]}$. These forces originate either from cellular acto-myosin contractility or from polymerization forces pushing membranes $^{[4]}$ (these latter forces are transmitted to the substrate on molecular clutches where actin filaments are connected to the substrates $^{[5]}$). Getting information on these forces is crucial if one wants to really understand individual as well as collective cell migration. These forces are now routinely accessible using techniques such as Traction Force Microscopy $^{[6,7]}$. They are often used as a simple direct readout, marker free, of cell contractile activity. However, a closer marker of this activity should be given by the the internal mechanical active stresses generated by cells, as some of the forces exerted on the plane could theoretically be the result of friction (i.e. passive forces, resulting from cell movements)$^{[8]}$. We explore in this paper the possibility of getting access to this active stresses examining the different techniques which have been developed for measuring stresses inside the monolayer.

We make explicit the origin of the stress each of these methods calculates, which indeed differs. We validate our approach using Finite Element Modeling of cells submitted to active forces. We show that these different methods allow to quantify the intracellular stress that resists cell active forces and the total intracellular stress accounting for both the active and the resistive stresses. Here we emphasize their complementarity and we make clear the limitations of these calculations. This article is a companion paper of an experimental usage of intracellular stress calculation $^{[9]}$.

II. MSM, BISM AND ISM CALCULATE DIFFERENT INTRACELLULAR STRESSES

Active forces in adherent cells generate both resistive forces inside the cells and outside, in the substrate underneath (see Fig. 1a–b). Taking advantage of the well-defined mechanical properties of the substrate, and following Ref. $^{[10]}$, several methods have been proposed that infer intracellular mechanical stresses from the measure of the resistive force field in the substrate $^{[11,12]}$ or the in-plane deformation field at the surface of the substrate $^{[13]}$. As we explain below, this allows quantifying the resistive stress from the cell body $^{[13]}$ or the total intracellular stress associated to the active and resistive intracellular forces $^{[11,12]}$.

The original idea of the mechanical approaches is to model cells as materials subjected to internal volume forces, the active forces mentioned above (acto-myosin contractility/polymerization). When the cells are adhered to a substrate, the internal forces are transmitted to the substrate and deform it. Assuming that cell colonies as well as single cells can be modeled as a thin plate, the mechanical equilibrium writes (Fig. 1):

\[ \vec{f}_{act} + \vec{f}_c - \vec{f}_m = \vec{0} \]  \hspace{1cm} (1)

with $\vec{f}_{act}$ the active cellular forces that cells build up following adhesion, $\vec{f}_c$ and $-\vec{f}_m$ respectively the reaction force of the cell body and the resistance of the deformable substrate opposed to these active forces, all modeled as surface forces because of the thin plate approximation. $\vec{f}_m$ is precisely the traction stress field measured by trac-
Mechanical equilibrium at an adhesion point: $f_{\text{act}}$ is the active force generated in the cell that reaches the adhesion, $S_c$ is the resistance opposed to its contraction (Fig. 1). Thus our aim is to characterize the stress field, $S_c$, that results from the strain of the adhered cell material in response to the active stress $f_{\text{act}}$. The active force generation following cell adhesion. This stress can be addressed by a gedanken experiment: let’s imagine that the cell could be detached without altering its active stress field, $S_{\text{act}}$. Then the cell body would contract till a new adhesion is formed, non specific adhesions or other types of adhesive machinery such as lectins [9, 19], the displacement field on top of the substrate. The displacement field is measured as in TFM, by the use of fluorescent markers embedded in the substrate. As a consequence of Eq. (5), implementation of ISM requires to know the Young’s modulus of the cell $E_c$ and its Poisson’s ratio $\nu_c$ but is independent of the thickness of the cell material [12].

Differently, Intracellular Stress Microscopy (ISM) addresses the quantification of the resistive component of the intracellular stress, $S_c$, that opposes the contraction of the adhered cell [13] (Fig. 1). When the cell is modeled as a thin elastic plate, it is straightly obtained by differentiating the displacement field of the neutral plane of the plate [17]. This approach can be extended to visco-elastic rheology when the cell material behaves like a Maxwell fluid, a rheological behavior that was for instance reported in flowing epithelial monolayers [18]. When the basal surface of the cell material is uniformly adhered to the substrate, either by integrin-mediated adhesions, non specific adhesions or other types of adhesive machinery such as lectins [9, 19], the displacement field of the neutral plane of the plate is identical to the displacement field on top of the substrate. The resistive stress then writes:

$$S_c = \left( \begin{array}{ccc} \sigma_{xx} & \sigma_{xy} & 0 \\ \sigma_{xy} & \sigma_{yy} & 0 \\ 0 & 0 & 0 \end{array} \right)$$

with

$$\begin{align*}
\sigma_{xx} &= \frac{E_c}{1-\nu_c^2} \left( \frac{\partial u_x}{\partial x} + \nu_c \frac{\partial u_y}{\partial y} \right) \\
\sigma_{yy} &= \frac{E_c}{1-\nu_c^2} \left( \frac{\partial u_y}{\partial y} + \nu_c \frac{\partial u_x}{\partial x} \right) \\
\sigma_{xy} &= \frac{E_c}{2(1+\nu_c)} \left( \frac{\partial u_x}{\partial y} + \frac{\partial u_y}{\partial x} \right)
\end{align*}$$

(x, y) are the in-plane coordinates, $E_c$ and $\nu_c$ are the Young’s modulus and the Poisson’s ratio of the cell material of thickness $h$, and $u_x, y$ are the in-plane components of the displacement field on top of the substrate. The displacement field is measured as in TFM, by the use of fluorescent markers embedded in the substrate. As a consequence of Eq. (5), implementation of ISM requires to know the Young’s modulus of the cell $E_c$ and its Poisson’s ratio $\nu_c$ but is independent of the thickness of the contractile plate, $h$.

MSM or BISM and ISM thus do not address the same intracellular stresses. MSM or BISM calculates the bidimensional total stress tensor $hS_{\text{tot}} = h(S_{\text{act}} + S_c)$ (Eq. (4)) while ISM quantifies the Young’s modulus-normalized resistive stress tensor $S_c/E_c$ (Eq. (5)).

In the following, by using 3D FEM, we compare the two approaches for calculating intracellular stresses and evaluate their consistency. The first approach was tested by using BISM and not MSM, as experimentally, TFM can only provide $f_m$ with a non negligible noise level of more (and often much more) than 10% [20], and BISM explicitly handles the noise level in its formulation. In
any case, as both MSM and BISM are based on the same
equation (Eq. 4), they should provide similar results as
already shown by Nier et al. [12].

III. USING 3D FEM TO COMPARE THE
DIFFERENT CALCULATIONS

FIG. 2. FEM calculation of intracellular stresses in an elastic
plate (\( E_c = 5 \text{kPa}, \nu_c = 0.5, h = 1 \mu\text{m} \)) bound to a deformable
substrate (\( E_s = 1 \text{kPa}, \nu_s = 0.5 \)). a) Schematics of the
numerical experiment. The plate is submitted to contractile
and tensile force dipoles respectively along the x and y axis
with truncated Gaussian profile (amplitude 1 kPa, standard
deviation 2 \( h \)) concentrated in 5 \( \mu\text{m} \) wide squared dots. b) Amplitude of the surface stresses \( f^c_m \) on the substrate. c) Comparison of the intracellular resistive stress \( S_c \) calculated with FEM and with ISM (\( S_{\text{ISM}} \), Eq. (5)). d) Comparison of the total intracellular stress \( S_{\text{tot}} = S_c - S_0 \) and BISM calculation \( S_{\text{BISM}} \) (Eq. (4)), regularization parameter \( L = 0.003 \). The inset shows the profiles of \( S_0 = -S_{\text{act}} \) and \( S_c \) used in the calculation of \( S_{\text{tot}} \).

Since MSM, BISM and ISM address different intracellu-
lar stresses, we built a finite elements simulation in order
to calculate these stresses. This approach had al-
ready been attempted in Nier et al. [12]. In this para-
graph we analyze this former simulation and show that
it can only compute \( S_c \) but not \( S_{\text{tot}} \). We then propose
a different simulation that allows obtaining \( S_c \) and \( S_{\text{tot}} \) from 3D FEM.

The simulation in Ref. [12] was conceived as follows:
the cell monolayer is modeled as a 2D square or disk of
either a pure viscous or elastic material. Cellular contrac-
tility is modeled as external forces (random dipoles dis-
tributed inside the geometry of interest). The substrate
is included in the simulation through its interaction
with the cells, and enters like a friction term proportional
to the velocity (viscous case) or to the displacement (elastic
case, the cells are then firmly attached to the substrate
composed of 1D springs). BISM and MSM stresses were
calculated by solving \( \text{div}S = \vec{t} \), with \( \vec{t} = -\vec{f}_{\text{act}} + \xi \vec{u} \)
being the forces that act on the cells and \( \vec{u} \) the displace-
ment field of the 2D material (note that there is a minus
sign error in the equation used in the supple-
mentary of Ref. [12]). Compared to Eq. (1), \( \vec{t} \) is therefore
the resistive force that opposes the active contraction,
\( \vec{t} = -\vec{f}_{\text{act}} + \vec{f}_m = \vec{f}_c \) and \( S = S_c \). Thus the model-
ning proposed in Ref. [12] allows to calculate the reac-
tive stress \( S_c \) by two means, either directly with differ-
entiating the displacement field (ISM approach, denoted
MSM in [12]) or by solving \( \text{div}S_c = \vec{f}_c \). Consistently,
BISM, MSM and ISM gave very similar results. Figure
S9 in Ref. [12] shows that the calculated stresses
localize identically for all the methods, either in the elas-
tic or in the viscous cases. Their amplitudes neverthe-
less differ but this indeed comes from different choices
of the rheological parameters in between the tests: for
instance, for the viscous case, first and second viscosities
are taken equal in the FEM simulation (\( \eta = \eta \prime \)) leading
to an equivalent Poisson’s ratio of 0.25 while the equiva-
 lent Poisson’s ratio is taken at 0.5 for MSM or ISM; in
the same way, the Young’s modulus of the cells chosen
for ISM and MSM differs from those chosen for BISM
(ISM: \( E_c = 1 \text{kPa}, \nu_c = 0.5, h \) not given, but the only value available is 5 \( \mu\text{m} \) leading to \( hE_c = 5 \text{kPa} \cdot \mu\text{m} \);
for MSM, \( E_c = 10 \text{kPa}, \nu_c = 0.5, h = 5 \mu\text{m} \), MSM
will then compare very well with the FEM simulation in
the elastic case as its result only depends on the value of
\( \nu_c \) and both are taken equal; BISM, in the elastic case,
\( hE_c = 100 \text{kPa} \cdot \mu\text{m} \) or \( hE_c = 10 \text{kPa} \cdot \mu\text{m} \) and \( \nu_c = 0.5 \).)
The reason for the failure of the previous simulation to
address both \( S_c \) and \( S_{\text{tot}} \) and model a true experiment
comes from the fact that \( S_{\text{tot}} \) is only meaningful when
the cells are adhered to a substrate. Otherwise, as de-
tailed in Section [11], \( S_{\text{tot}} = 0 \) as the intracellular resistive
stress \( S_c \) balances the active stress \( S_{\text{act}} \) in the absence
of anchorage to a substrate, \( \vec{f}_{\text{act}} + \vec{f}_c = 0 \) (Fig. [1]).

To solve this issue, we thus proposed a model where
the cell (or equivalently the cell colony) is modeled as
thin plate uniformly bound to the substrate (Fig. 2).
The dimensions of the thin plate were chosen so that
the deformation field is fairly uniform in the thickness
of the cellular material (square elastic sheet of size 30 \times
30 \( \mu\text{m}^2 \) and 1 \( \mu\text{m} \) in thickness). We focused on the elastic
case, with Young’s modulus \( E_c = 5 \text{kPa} \) and a Poisson’s
ratio \( \nu_c = 0.5 \). The thin plate is sitting on top of an
elastic gel (the substrate) which is modeled as a thick
elastic parallelepiped (size 200 \times 200 \times 100 \( \mu\text{m}^3 \) in \( x, y, z \),
with Young’s modulus \( E_m = 1 \text{kPa} \) and a Poisson’s ratio
\( \nu_m = 0.5 \)). A contractile dipole is positioned along the
x-axis, composed of Gaussian forces of amplitude 1 kPa
and width \( \sigma \) adjusted between 0.25 and 2 \( \mu\text{m} \). A tensile
dipole is set on the y-axis with the same amplitude and
width.
IV. DETAILS ON THE ROBUSTNESS OF ISM AND BISM CALCULATIONS

A. Calculation methods

The 3D FEM calculation provides the displacement field at the interface between the cell and the substrate. This displacement field was used to calculate the intracellular stresses $S_c$ and $S_{tot}$ using ISM and BISM as would be done with experimental data [9]. The sampling was chosen following Shannon criterion: the displacement field was interpolated on a sampled regular grid with a frequency more than twice the maximal frequency obtained from the FEM calculation. The resistive stress field $S_c$ was obtained from ISM, by differentiating the in-plane displacement field retrieved from the 3D FEM calculation using a Sobel approximation of the derivative (Eq. (5)). $S_{tot}$ was obtained from BISM by solving Eq. (4). Traction stresses $f_m$ were first calculated using Fast Fourier Transform, following Butler et al. [12]. We took $\nu = 0.49$ for the calculations. The total intracellular stress $S_{tot}$ was then calculated following Ref. [12]. As it is quite demanding on computer memory, we used a grid of 50 × 50 pixels to calculate the stress, which enables a rather fast computation, so as to perform many different tests in a reasonable amount of time. Boundary conditions were enforced in the prior to correspond to the different tests in a reasonable amount of time. Boundary conditions were enforced in the prior to correspond to the different tests in a reasonable amount.

B. Choosing the regularization parameter in BISM

As detailed in Ref. [22], the choice of the optimal parameter for equation form like Eq. (4) is far from obvious. It is to be noted that the L-curve criterion is not consistent with the Morozov discrepancy principle here (which states that Eq. (4) can not be solved with a better accuracy than the noise on $f_m$), as it gives a dominant weight to the accuracy of the equilibrium equation Eq. (4), omitting that the right-hand term, $f_m$ is a noisy, inaccurate data. We thus chose to calculate the regularization parameter $L$ using the $\chi^2$ estimate [7] which considers the noise level of the right-hand term in Eq. (4). In BISM, this criterion expresses as $L = (\ell^2s^2/s_0^2$, with $\ell$ the size of the grid sampling for the calculation of $S_{tot}$, $s$ the standard deviation of the noise of $f_m$, and $s_0$ the standard deviation of the calculated stress $hS_{tot}$ [12]. Since $s_0$ is unknown, an additional criterion is required. Based on Eq. (4), we estimated $s_0 \simeq \ell s_1$, with $s_1$ the standard deviation of $f_m$. Then $L$ is simply obtained from $f_m$, stress field distribution and the quantification of its noise level out of the cell boundaries:

$$L = s^2/s_1^2$$

To calculate the noise, we used the values of the surface forces $f_m$ outside of the cell boundaries (it should be zero if the calculation was perfect, which of course is not the case.) However, the calculation appeared trickier than for real data coming from experiments. Here, the noise level sharply decreased with distance from the plate. Thus defining the proper position of the boundary appeared mandatory to ensure that the captured noise is not the spread force signal unavoidable with finite element calculation but still is representative of FEM-induced noise. This issue is specific to FEM calculation and is not met in experimental cases where the noise around the cell is fairly uniform (see [9]). To this end, noise statistics was quantified out of the cell in regions whose distance to cell edges was varied. $L$ values were then obtained with Eq. (9) in dependence on this distance (Fig. 3). $L$ was considered optimal at the maximal curvature of this decreasing curve as it is the place of best compromise between attenuated force signal and maximal noise level. For the values modeled in Fig. 2a, we obtained a regularization parameter $L = 0.002$ which consistently corresponds to the best choice for the regularization parameter compared to FEM calculation of $S_{tot}$ (Fig. 2c).

FIG. 3. Understanding BISM. a) L values calculated with Eq. (5), with $s$ being the noise level outside of the cell quantified in a mask at a distance $d$ from the plate boundaries. The optimum for $L$ is chosen at the maximum of curvature in the curve. b) Increasing the regularization parameter in BISM calculation filters the low frequencies. The colors refer to values of the regulation parameter. c) Boundary conditions are given by the surface forces $f_m$ at the edges of the plate. b) Zero stress is assumed at the edges of the plate. The optimum for $L$ is chosen at the maximum of curvature in the curve. d) Increasing the regularization parameter in BISM calculation filters the low frequencies. The colors refer to values of the regulation parameter. The other colors refer to values of the regularization parameter.

C. Effect of noise in the calculation of $S_{tot}$ and $S_c$

Noise strongly impacts the calculation of the force field in TFM. This problem was addressed by using a Bayesian
approach [23], a regularization scheme [7] or a filtering in the Fourier space [21]. These regularization schemes were shown to filter high frequencies [20, 24]. Noise issues keep also critical in the calculation of the intracellular stresses and we questioned how noise impacts ISM and BISM calculations. ISM is based on the derivative of the displacement field. It is therefore very sensitive to high frequency noise. A filtering is applied by the use of the Sobel approximation in the calculation of the gradients. We showed in a companion paper [9] that experimentally, the dispersions of \( \text{div} S_c \) and \( \vec{f}_m \) are similar. The fact that \( \text{div} S_c \) does not show many points with high amplitude out of the fit line shows that ISM is not altered by high frequency noise compared to TFM. Differently, BISM calculation is based on the integration of the surface force field \( \vec{f}_m \). A perturbation in \( \vec{u} \) with wave vector \( \vec{q} \) results in a perturbation of the stress tensor \( \Delta S_{\text{tot}} \) proportional to \( 1/\vec{q} \). Low frequency noise thus strongly alters the value of \( S_{\text{tot}} \). And indeed, the regularization scheme in BISM calculation damps these low frequencies (Fig. 3b). Thus in this context, BISM is expected to be very sensitive to the boundary conditions.

D. Effect of boundaries conditions on BISM calculations

A proper choice of the boundary conditions also appeared to be critical for the success of BISM calculation. \( S_{\text{tot}} \) was either calculated when assuming zero stress at the edge of the thin plate or when fixing the boundary stress with the surface forces at the edge of the plate: \( S_{\text{tot}} \cdot \vec{n} = \vec{f}_m \), with \( \vec{n} \) the normal to the edge of the plate. Only the appropriate boundary conditions brought the BISM curve close to the FEM curve (Fig. 3a–d).

V. BISM AND ISM ARE CONSISTENT WITH FEM

Stresses calculated with ISM and BISM approaches were compared to the FEM calculation. While \( S_c \) is a direct output of the FEM stress tensor calculation, \( S_{\text{tot}} \) was calculated as the difference between the resistive stress tensors of the adhered plate (\( S_c \)) and of the non adhered plate (\( S_0 = -S_{\text{act}} \)) as described in Sec. IV. It was compared to BISM calculation whose value of the regularization parameter was chosen based on the noise level of \( \vec{f}_m \).

As shown on Fig. 2a, \( S_{\text{ISM}} \) compared well with \( S_c \) in consistence with the thin plate assumption. Similarly, BISM did reconstruct \( S_{\text{tot}} \) by using appropriate boundary conditions and regularization parameter (Fig. 2b), both parameters having an important impact on the stress calculation as was detailed above.

VI. RELATIONSHIP BETWEEN DIV S AND F

In [9], we experimentally evidenced a linear relationship between \( \text{div} S_c \) and \( \vec{f}_m \), which entails another linear relationship between \( S_c \) and \( S_{\text{tot}} \). We showed that these linear relationships could only be observed if the sizes of the adhesive active areas were smaller than the resolution of our analysis (\( \text{i.e.} \ 400\text{nm at best} \)). Here our patches are necessarily above the resolution of our grid. But, we did try to run our modelling on a smaller Gaussian adhesive patch of \( 1\mu\text{m} \) in size. Results are presented on Fig. 4. Again BISM and ISM are nicely recovered (Fig. 4a and b) but we do not recover the linear relationship between \( \text{div} S_c \) and \( \vec{f}_m \) (Fig. 4b). This is normal as the size of the patches are necessarily larger than the sampling size fixed by the mesh. However, when reducing these sizes, the relationship tends toward more linear (compare the blue and red lines).

VII. CASE OF LOCALIZED ADHESION

We then examined the case where the cells do not adhere everywhere. We tested how this situation would impact the correlation between \( \text{div} S_{\text{ISM}} \) and \( \vec{f}_m \). It should be noted that out of the areas where the cell is adhered,
VIII. CONCLUSION

We proposed here a set of 3D FEM simulations to test and validate intracellular stress calculations that are done by two independent techniques, ISM and BISM, which addresses two different stresses. We showed that BISM enables to measure the total stress inside the cells, while ISM retrieves the resistive component of the stress. We delineated the framework within which these techniques provide consistent information: for both techniques, the calculation infers relevant stresses only at the locations where the cells are adherent; concerning BISM, a proper quantification of the noise level to select the optimal regularization parameter and a proper definition of the boundary conditions are mandatory. Within this well-defined framework, we have shown that both approaches bring valuable and complementary information on intracellular stresses which then allow the retrieval of the active part of the intracellular stress. Taking advantage of this knowledge, it is now possible to analyze intracellular stresses in real experiments. This is what we have done in a companion paper [9].

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