Cytoplasmic Streaming due to Active Surface Flows

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Abstract

We study the flows induced inside the bulk of a cell given a flow pattern on the surface of a cell.For this,we use a spherical model of the cell with the active component only at the surface of the cell.This model is exactly solvable and we can compute the flow patterns inside the cytoplasm .The low Reynolds number regime allows us to solve Stokes equation by using vector spherical harmonics to compute the velocity field inside the cell at anypoint and on any sphere in general inside the surface on which the velocity is specified.

1.Introduction

Fluid flows are actively involved in processes taking place inside living organisms .They affect a lot of physical,chemaical and biological processes which are responsible for the mechanics of these organism.These flows are present at various scales in living organisms and have different roles to play.When talking about living organisms,these fluids can be both at large scales as blood flowing in veins and small scales as cytoplasm inside a cell.Flows at different scales affect various proceses differently.One of the interesting flows are at at the cellular level which are called intracellular flows,also called Streaimg.These flows inside a cell are very essential as they affect a mariad of processes such as transport of material and information from one part of it cell to another part and convective transport of proteins and other chemical species.Proteins and chemical species can get coupled to these flows and get redistributed which in turn can effectively help in breaking the symmentry by mechano-chemical process and lead the cell to determine chemical axis for further growth and development. The diffusion process is not very effective candidate as we know that the cytoplasm is very dense and so diffusion dependent processeswould take long timescales compared the cell growth.It turns out they are there should be other mechanism such as Streaming.These flows have been measured in labs inside real cells which are interesting and stimulating. So studying these flows as to how they govern the dynamics inside a cell is important.

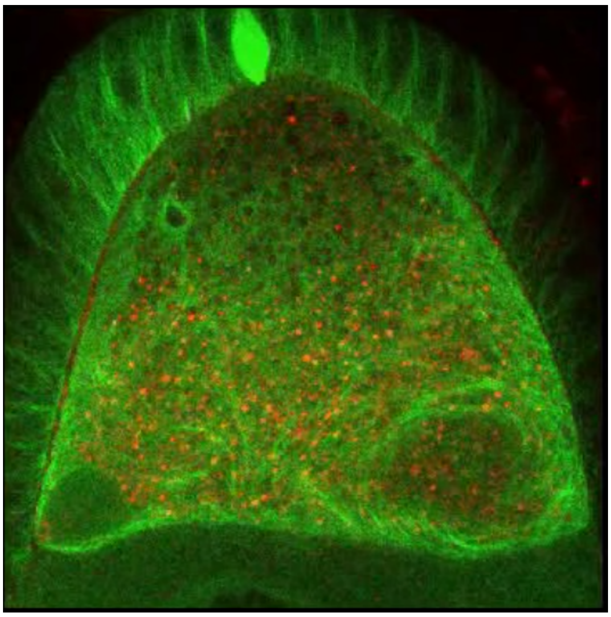


Figure 1: Here is a image of cytoplasmic streaming in Drosophila due to activity of motors obtained by Particle Imaging Velocimetry.The spiral kind of structure near the right bottom inside the cell is due to streaming.

2.The Cell Structure :How a Physicist views it

The Cell is a very complex system,far more complex than the usual physical systems which are studied and dealt in the main stream physics.With the enormous number of components,along with the fact that they are out of equilibrium system makes them complicated.The model of the cell,can be broken down and modeled with concepts from condensed matter physics,non-equilibrium statistics,fluid dynamics,mechanics,nonlinear and complex systems.Thus biological systems like cell turns out to be more rich and offer more challenge to study them.And hence many problms can be addressed by studying the minimal model of the cell and bring out the physics behind various life governing proceses at the fundamental level. A typical Cell consists of cytoskeleton,nucleus and other organalles and various kinds of proteins.The cytoskeleton has a filamentous strucure.But at time scales higher than the material turnover scales,we can study cytoskeleton as an active fluid,with the active components sparsly populated in the bulk and densly polulated near the cell membrane.

3.The Actomyosin Cortex as Active Matter

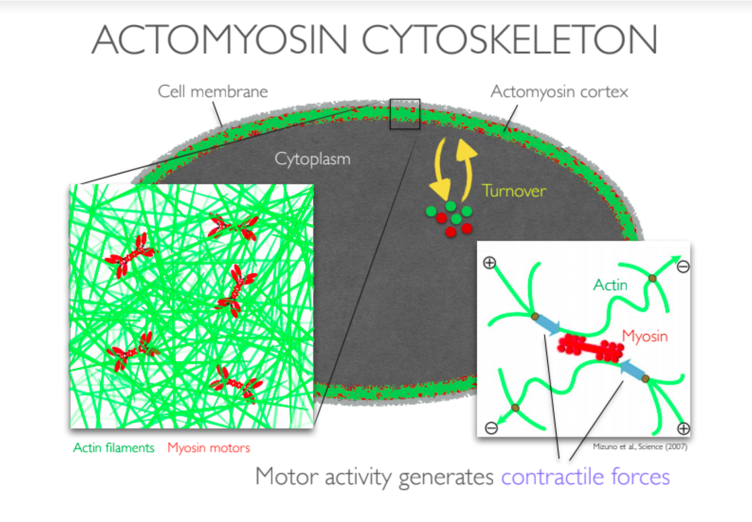


Figure 2: A schematic diagram of the actomyosin cortex is shown.

The actomyosin cortex is a thin layer with mesh of filaments with myosin motors just beneath the plasma membrane. The Cytoskeleton is a network of filamentous proteins and the motors.These motors consume energy and move along these filmentous structures and by pulling them,locally generating stress(contractile in nature) .Thus there are intrinsic forces and hence this make active matter out of equilibrium systems. Also there is continuous turnover of actomyosin with the cytoplasm in the bulk.Over timescales higher than this turnover,we can model this thin actomyosin cortex as a thin layer of active viscoelastic fluid near the cell membrane which is capable of generating stress .Thus the stress generated at a point near the cell membrane is proportional to the concentration of the actomyosin motors and their orientation.

4.Fluid Dynamics in Low Reynolds Number:Stokes Equation

As discussed above,the cytoplasm can treated as a fliud and so we can write Navier-Stokes equation for the cell. But the typical flows experimentally observed inside the cell is of the order of 10μm minute^{-1},and the typical dimension of the cell being 10-100 μm and the viscosity and density of the cytoplasm being higher than water.Now that we see that the Reynolds number is of the order of 10^{-6}.Thus in this regime,the Navier-Stokes equation can be modified to Stokes Equation.This can be easily shown below. The Navier Stokes equation ,

$$\rho\left(\frac{\partial \mathbf{V}}{\partial t}+\mathbf{V}\cdot\nabla\mathbf{V}\right)=-\nabla p+\mu\,\nabla^2\mathbf{V}+\tfrac{1}{3}\mu\,\nabla(\nabla\cdot\mathbf{V})+\rho\mathbf{g}$$

(1)

Where,

$\mathbf{V}$ =velocity
ρ =density
g=acceleration due to gravity
p=pressure

We have taken the fluid incompressible, $\nabla\cdot\mathbf{V}=0$ with no body force,

$$\rho\left(\frac{\partial \mathbf{V}}{\partial t}+\mathbf{V}\cdot\nabla\mathbf{V}\right)=-\nabla\bar{p}+\mu\,\nabla^2\mathbf{V}+\rho\mathbf{g} \tag{2}$$

We can make our equation dimensionless as below by scaling the variables $\mathbf{v}=U\bar{v}$,$t=T\bar{t}$ and the del and laplacian operators as $\frac{1}{L}$ and $\frac{1}{L^2}$ respectively, also putting T= $\frac{L}{U}$,we get

$$\frac{\rho UL}{\mu}\left(\frac{\partial\bar{v}}{\partial\bar{t}}+\bar{v}\cdot\nabla\bar{v}\right)=-\frac{L\nabla\bar{p}}{\mu U}+\nabla^2\bar{v} \tag{3}$$

Thus,when Reynolds number is of the order of 10^{-6},we can neglect the nonlinear terms multiplied by the Reynolds number and hence we get Stokes equation

$$-\nabla\bar{p} + \mu\,\nabla^2\mathbf{V} = 0 \tag{4}$$

The advantage of the Stokes equation is that it is a linear Partial differental Equation.Thus flow is completely determined and is unique for a specific set of boundary conditions. Another important aspect is that there is no time evolution of the flows.Hence the flows can be thought of determined immediately by specifying the flows on the surface. The flows generated on the surface of the cell driven by the coupling of the Actomysin concentration and the flows on the surface.These flows when coupled to bulk can determine the flows field in the cyoplasm.Thus given a surface velocity on the cell,we can compute this field by using Stokes Equation.

5.The Spherical Geometry: A simple model of the cell

The Real cells as we know have arbitrary geometry.So it is impossible to solve the flow field analytically for a real cell. The simplest model we can think of whose analytical solutions can be determined is a cell of spherical geometry. This simple geometry can give us the general picture of the flow fields inside and further study can be build on it based on purturbative calculations or numerical methods.For cells of arbitrary geometry,we can use finite element method to compute the flow field.

Here we exploit the Vector Spherical Harmonics to solve for the velocity field in the bulk for a spherical cell. The boundary conditions we take for our model is that there is no radial velocity at the surface of the cell i.e. only tangential velocity is allowed at the surface of the cell so that the flow is contained within the spherical geometry.Also the velocity at the center of the cell can only be radial due to the fact that there can be no θ or ϕ direction at the center. Also in calculation,we will neglect the $\ell = 0$ mode as it only represents the averaged velocity over the surface of the sphere,which can be shifted to zero by galilean transformation to the cell's frame of reference.

6.Vector Spherical Harmonics

To express a field in spherical coordinates,we need basis functions in terms of which our velocity field can be expressed. These are vector functions be derived from the scalar spherical harmonics Y_{lm} as follows:

$$\mathbf{Y}_{lm} = Y_{lm}\hat{\mathbf{r}} \tag{5}$$
$$\mathbf{\Psi}_{lm} = r\nabla Y_{lm} \tag{6}$$
$$\mathbf{\Phi}_{lm} = \mathbf{r} \times \nabla Y_{lm} \tag{7}$$

Vector Spherical Hamrmonics are eigen functions of the Vector Laplacian Operator or Laplace de-Rham operator. Curl and Laplacian of these functions have nice properties which can be exploited to solve the Stokes Equation inside the sphere.Also they are orthogonal at any point (r, θ, ϕ) on a sphere and are also orthogonal in Hilbert space. Some properties of these Vector Spherical Harmonics are listed here:

6.1 Divergence

$$\nabla \cdot (f(r)\mathbf{Y}_{lm}) = \left(\frac{\mathrm{d}f}{\mathrm{d}r} + \frac{2}{r}f\right) Y_{lm} \tag{8}$$
$$\nabla \cdot (f(r)\mathbf{\Psi}_{lm}) = -\frac{l(l+1)}{r} f Y_{lm} \tag{9}$$
$$\nabla \cdot (f(r)\mathbf{\Phi}_{lm}) = 0 \tag{10}$$

6.2 Curl

$$\nabla \times (f(r)\mathbf{Y}_{lm}) = -\frac{1}{r} f \mathbf{\Phi}_{lm} \tag{11}$$
$$\nabla \times (f(r)\mathbf{\Psi}_{lm}) = \left(\frac{\mathrm{d}f}{\mathrm{d}r} + \frac{1}{r}f\right) \mathbf{\Phi}_{lm} \tag{12}$$
$$\nabla \times (f(r)\mathbf{\Phi}_{lm}) = -\frac{l(l+1)}{r} f \mathbf{Y}_{lm} - \left(\frac{\mathrm{d}f}{\mathrm{d}r} + \frac{1}{r}f\right) \mathbf{\Psi}_{lm} \tag{13}$$

7. Analytical Calulation for the bulk

A velocity field at any point (r, θ, ϕ)can be expanded in vector spherical harmonics as follows :

$$\mathbf{V} = \sum_{l=0}^{\infty} \sum_{m=-l}^{l} \left(V_{lm}^{Y}(r)\mathbf{Y}_{lm} + V_{lm}^{\psi}(r)\mathbf{\Psi}_{lm} + V_{lm}^{\phi}(r)\mathbf{\Phi}_{lm}\right) \tag{14}$$

In more compact form,we can write them as:

$$\mathbf{V} = \mathbf{V}^{Y} + \mathbf{V}^{\psi} + \mathbf{V}^{\phi} \tag{15}$$

Where,

$$\mathbf{V}^Y = \sum_{l=0}^{\infty} \sum_{m=-l}^{l} V_{lm}^Y(r)\mathbf{Y}_{lm} \tag{16}$$

$$\mathbf{V}^\psi = \sum_{l=0}^{\infty} \sum_{m=-l}^{l} V_{lm}^\psi(r)\mathbf{\Psi}_{lm} \tag{17}$$

$$\mathbf{V}^\phi = \sum_{l=0}^{\infty} \sum_{m=-l}^{l} V_{lm}^\phi(r)\mathbf{\Phi}_{lm} \tag{18}$$

We take vector Laplacian of the velocity with the rules that,

$$\Delta\left(v(r)\mathbf{Z}_{lm}\right) = \left(\frac{1}{r^2}\frac{\partial}{\partial r}r^2\frac{\partial V}{\partial r}\right)\mathbf{Z}_{lm} + v(r)\Delta\mathbf{Z}_{lm} \tag{19}$$

$$\mathbf{Z}_{lm} = \mathbf{Y}_{lm}, \mathbf{\Phi}_{lm}, \mathbf{\Psi}_{lm} \tag{20}$$

where Z can take the values

$$\mathbf{Z}_{lm} = \mathbf{Y}_{lm}, \mathbf{\Psi}_{lm}, \mathbf{\Phi}_{lm} \tag{21}$$

$$\Delta\mathbf{Y}_{lm} = -\frac{1}{r^2}(2 + l(l+1))\mathbf{Y}_{lm} + \frac{2}{r^2}\mathbf{\Psi}_{lm} \tag{22}$$

$$\Delta\mathbf{\Psi}_{lm} = \frac{2}{r^2}l(l+1)\mathbf{Y}_{lm} - \frac{1}{r^2}l(l+1)\mathbf{\Psi}_{lm} \tag{23}$$

$$\Delta\mathbf{\Phi}_{lm} = -\frac{1}{r^2}l(l+1)\mathbf{\Phi}_{lm} \tag{24}$$

Thus operating the vector laplacian on the velocity,we get

$$\Delta\mathbf{V} = \sum_{z=r,\psi,\phi} \sum_{l=0}^{\infty} \sum_{m=-l}^{l} \left(\frac{1}{r^2}\frac{\partial}{\partial r}r^2\frac{\partial v^z}{\partial r}\right)\mathbf{Z}_{lm} + v(r)\Delta\mathbf{Z}_{lm} \tag{25}$$

We can use compact notation to simplify further as follows: Let

$$F^z = \left(\frac{1}{r^2}\frac{\partial}{\partial r}r^2\frac{\partial V^z}{\partial r}\right) \tag{26}$$

Using the identities (5),(6) and (7) in equation ,we seperate the cofficients of the three VSH as,

$$(\mathbf{\Delta V})_{lm}^Y = F^Y - \frac{2 + (l(l+1)}{r^2}V_{lm}^Y + \frac{2(l(l+1))}{r^2}V_{lm}^\psi = P_{lm} \tag{27}$$

$$(\mathbf{\Delta V})_{lm}^\psi = F^\psi + \frac{2}{r^2}V_{lm}^Y - \frac{(l(l+1))}{r^2}V_{lm}^\psi = Q_{lm} \tag{28}$$

$$(\mathbf{\Delta V})_{lm}^\phi = F^\phi - \frac{(l(l+1))}{r^2}V_{lm}^\phi = R_{lm} \tag{29}$$

Expressing the laplacian of the velocity in compact form as:

$$(\Delta \mathbf{V})_{lm} = P_{lm}\mathbf{Y}_{lm} + Q_{lm}\mathbf{\Psi}_{lm} + R_{lm}\mathbf{\Phi}_{lm} \tag{30}$$

Now,taking curl of the laplacian of the velocity using the standard identities,we have :

$$\nabla \times (P\mathbf{Y}_{lm}) = -\frac{1}{r}P\mathbf{\Phi}_{lm} \tag{31}$$

$$\nabla \times (Q\mathbf{\Psi}_{lm}) = \left(\frac{\mathrm{d}Q}{\mathrm{d}r} + \frac{1}{r}Q\right)\mathbf{\Phi}_{lm} \tag{32}$$

$$\nabla \times (R\mathbf{\Phi}_{lm}) = -\frac{l(l+1)}{r}R\mathbf{Y}_{lm} - \left(\frac{\mathrm{d}R}{\mathrm{d}r} + \frac{1}{r}R\right)\mathbf{\Psi}_{lm} \tag{33}$$

Thus we have the curl of the laplacian as:

$$\nabla \times (\nabla^2 \mathbf{V})_{lm} = -\frac{l(l+1)}{r}R\mathbf{Y}_{lm} - \left(\frac{\mathrm{d}R}{\mathrm{d}r} + \frac{1}{r}R\right)\mathbf{\Psi}_{lm} + \left(-\frac{1}{r}P + \frac{\mathrm{d}Q}{\mathrm{d}r} + \frac{1}{r}Q\right)\mathbf{\Phi}_{lm} \tag{34}$$

From the Orthogonality and linear Independence of VSH's,each term in the brackets must be identicaly zero . Thus we get the differential equations as :

$$\frac{l(l+1)}{r}R = 0 \tag{35}$$

$$\left(\frac{\mathrm{d}R}{\mathrm{d}r} + \frac{1}{r}R\right) = 0 \tag{36}$$

$$\left(-\frac{1}{r}P + \frac{\mathrm{d}Q}{\mathrm{d}r} + \frac{1}{r}Q\right) = 0 \tag{37}$$

We can now expand the two equations and removing the redundant equations , we get

$$\left(\frac{1}{r^2}\frac{\partial}{\partial r}r^2\frac{\partial V^{\phi}_{lm}}{\partial r}\right) - \frac{(\ell(\ell+1))}{r^2}V^{\phi}_{lm} = 0 \tag{38}$$

$$-\frac{1}{r}P + \frac{\mathrm{d}Q}{\mathrm{d}r} + \frac{1}{r}Q = 0 \tag{39}$$

The general Solution to equation(23) is:

$$V^{\phi}_{lm} = A^l_m r^{\ell} + B^l_m r^{-(\ell+1)} \tag{40}$$

With the condition that at $r = 0$, $V^{\phi}_{lm} = 0$,$B^{l}_{m} = 0$.Hence the general solution to $\mathbf{V}^{\phi}$ is :

$$\mathbf{V}^{\phi} = \sum_{l=1}^{\infty} \sum_{m=-l}^{l} A^{l}_{m} r^{\ell} \mathbf{\Phi}_{lm} \tag{41}$$

Equation (39) can be expanded as ;

$$\frac{\mathrm{d}}{\mathrm{d}r}\left(F^{\psi} + \frac{2}{r^2}V^{Y} - \frac{\ell(\ell+1)}{r^2}V^{\psi}\right)$$
$$+\frac{1}{r}\left(F^{\psi} + \frac{2}{r^2}V^{Y} - \frac{\ell(\ell+1)}{r^2}V^{\psi}\right) - \frac{1}{r}\left(F^{r} - \frac{2+(\ell(\ell+1)}{r^2}V^{Y} + \frac{2\ell(\ell+1)}{r^2}V^{\psi}\right) = 0 \tag{42}$$

We have simplified with the assumption that the flow is incompressible

$$\nabla \cdot \mathbf{V} = 0 \tag{43}$$

$$\nabla \cdot \mathbf{V} = \sum_{l=0}^{\infty} \sum_{m=-l}^{l} \left(\frac{\mathrm{d}V^{Y}_{lm}}{\mathrm{d}r} + \frac{2}{r}V^{Y}_{lm} - \frac{l(l+1)}{r}V^{\psi}_{lm}\right)\mathbf{Y}_{lm} \tag{44}$$

$$\Rightarrow \quad \left(\frac{\mathrm{d}V^{Y}_{lm}}{\mathrm{d}r} + \frac{2}{r}V^{Y}_{lm} - \frac{l(l+1)}{r}V^{\psi}_{lm}\right) = 0 \tag{45}$$

The equation (28) can be simplified as follows:

$$\frac{r^3\partial^3}{\partial r^3}V^{\psi}_{lm} + \frac{3r^2\partial^2}{\partial r^2}V^{\psi}_{lm} - \frac{l(l+1)r\partial}{\partial r}V^{\psi}_{lm} - \frac{r^2\partial^2}{\partial r^2}V^{Y}_{lm} + \ell(\ell+1)\left(V^{Y}_{lm} - V^{\psi}_{lm}\right) = 0 \tag{46}$$
$$\tag{47}$$

For the velocity component V^{ϕ}_{lm} and V^{r}_{lm}.Equation (31) and (32) are coupled differential equations and reduce to euler form of differentail equation.The simplified equations are solvable. Using the incompressibility condition , we get the ordinary differential equation below.

$$\frac{r^4\partial^4}{\partial r^4}V^{Y}_{lm} + \frac{8r^3\partial^3}{\partial r^3}V^{Y}_{lm} - \frac{12 - 2\ell(\ell+1)r^2\partial^2}{\partial r^2}V^{Y}_{lm} - \frac{4\ell(\ell+1)r\partial}{\partial r}V^{Y}_{lm} + ((\ell(\ell+1))^2 - 2\ell(\ell+1))V^{Y}_{lm} = 0 \tag{48}$$

The above is an Euler-Lagrange type differential equation and can be solved by substituting $r = e^{z}$ and then transforming the ode into the following form:

$$\frac{\partial^4}{\partial z^4}V^{Y}_{lm} + \frac{2\partial^3}{\partial z^3}V^{Y}_{lm} + \frac{-2 - \ell(\ell+1)\partial^2}{\partial z^2}V^{Y}_{lm} + \frac{(-1 - 3\ell(\ell+1))\partial}{\partial z}V^{Y}_{lm} + ((\ell(\ell+1))^2 - 2\ell(\ell+1))V^{Y}_{lm} = 0 \tag{49}$$

The solution to this has the form:

$$V_{lm}^{Y} = C_1^{\ell} r^{\ell-1} + C_2^{\ell} r^{\ell+1} + C_3^{\ell} r^{-\ell} + C_4^{\ell} r^{-(\ell+2)} \tag{50}$$

The Boundary condition inside the cell i.e finite at centre and zero at the surface does not permit solutions which diverge at the centre. The cofficients C_1^0 and C_4^0 must vanish and C_3^{ℓ} and C_4^{ℓ} must vanish for all $\ell > 1$. The solution thus retained must be of the form

$$V_{lm}^{Y} = \begin{cases} C_2^0 r + C_3^0, \ell = 0 \\ C_1^{\ell} r^{\ell-1} + C_2^{\ell} r^{\ell+1}, \ell > 0 \end{cases}$$

At the surface of the cell $r = R$,the radial velocity must be zero.This condition must be satisfied individually for every mode present i.e. for each value of ℓ. Using this condition,we get for $\ell = 0$ mode $C_3^0 = -C_2^0 R$ and for $\ell > 0$ modes ,$C_1^l = -C_2^l R^2$

$$\mathbf{V}^{Y} = C_2^0 (r - R)\mathbf{Y}_{00} + \sum_{l=1}^{\infty} \sum_{m=-l}^{m=l} C_2^l \left(r^{\ell+1} - R^2 r^{\ell-1}\right) \mathbf{Y}_{lm} \tag{51}$$

Now from the incompressibility condition,we have :

$$\frac{\mathrm{d}V_{lm}^{Y}}{\mathrm{d}r} + \frac{2}{r} V_{lm}^{Y} - \frac{\ell(\ell+1)}{r} V_{lm}^{\psi} = 0 \tag{52}$$

This condition can be used to dtermine V_{lm}^{r} along with the condition that at r= 0, $V_{lm}^{\psi} = 0$,we find that only $\ell >= 1$ and higher modes exist.

$$\mathbf{V}^{\psi} = \sum_{l=1}^{\infty} \sum_{m=-\ell}^{\ell} C_m^{\ell} \left(-\frac{R^2 r^{\ell-1}}{\ell} + \frac{r^{\ell+1}(\ell+3)}{\ell(\ell+1)} \right) \mathbf{\Psi}_{lm} \tag{53}$$

Also the equation(42) changes as

$$\mathbf{V}^{Y} = \sum_{l=1}^{\infty} \sum_{m=l}^{m=-l} C_2^l \left(r^{\ell+1} - R^2 r^{\ell-1}\right) \mathbf{Y}_{lm} \tag{54}$$

Given any cortical flow of the form:

$$\mathbf{V}_s = \sum_{l=1}^{\infty} \sum_{m=-l}^{l} \left(v_{lm}^{\psi} \mathbf{\Psi}_{lm} + v_{lm}^{\phi} \mathbf{\Phi}_{lm} \right) \tag{55}$$

Now,given that we have the cortical Velocity we can determine the cofficients C^l_m and A^l_m by matching the general velocity at $r = R$ for $\ell >= 1$

$$A^l_m = \frac{v^{\phi}_{lm}}{R^{\ell}} \tag{56}$$

$$C^l_m = \frac{\ell(\ell+1)v^{\psi}_{lm}}{2R^{\ell+1}} \tag{57}$$

Once we have determined these cofficients,we can build the bulk flow inside the sphere. Comparing equation (3),(4),(5) with (28),(40),(41),we get

$$V^Y_{lm} = C^{\ell}_m \left(r^{\ell+1} - R^2 r^{\ell-1}\right) \tag{58}$$

$$V^{\psi}_{lm} = C^{\ell}_m \left(-\frac{R^2 r^{\ell-1}}{\ell} + \frac{r^{\ell+1}(\ell+3)}{\ell(\ell+1)}\right) \tag{59}$$

$$V^{\phi}_{lm} = A^{\ell}_m r^{\ell} \tag{60}$$

Also, We can expand $\mathbf{\Psi}_{lm}$ and $\mathbf{\Phi}_{lm}$ in terms of scalar Y_{lm} as

$$\mathbf{\Psi}_{lm} = \frac{\partial Y_{lm}}{\partial \theta}\hat{\theta} + \frac{\partial Y_{lm}}{\sin\theta \partial \phi}\hat{\phi} \tag{61}$$

$$\mathbf{\Phi}_{lm} = -\frac{\partial Y_{lm}}{\partial \theta}\hat{\phi} + \frac{\partial Y_{lm}}{\sin\theta \partial \phi}\hat{\theta} \tag{62}$$

Thus we can write the velocity back in terms of r, θ, ϕ basis as:

$$\mathbf{V} = \sum_{lm} \left(V^Y_{lm} Y_{lm}\right)\hat{r} + \left(V^{\psi}_{lm}\frac{\partial Y_{lm}}{\partial \theta} + \frac{V^{\phi}_{lm}\partial Y_{lm}}{\sin\theta \partial \phi}\right)\hat{\theta} + \left(V^{\psi}_{lm}\frac{\partial Y_{lm}}{\sin\theta \partial \phi} - \frac{V^{\phi}_{lm}\partial Y_{lm}}{\partial \phi}\right)\hat{\phi} \tag{63}$$

8.Calculation of Stress Tensor

We can compute the Stress generated by the flows inside the sphere by the expression :

$$[\sigma] = \eta\left(\nabla\mathbf{V} + (\nabla\mathbf{V})^{\mathbf{T}}\right) \tag{64}$$

where

$$\nabla = \hat{r}\frac{\partial}{\partial r} + \hat{\theta}\frac{\partial}{r\partial\theta} + \hat{\phi}\frac{\partial}{r\sin\theta\partial\phi} \tag{65}$$

The two simple cases where we can easily compute the independent components of the stress tensor are given below:

Case I : All C_{lm} are zero

In this case we have only V^{ϕ}_{lm} non-zeros. The Velocity field reduces to the form:

$$\mathbf{V} = \sum_{lm} \left(V^{\phi}_{lm} \frac{\partial Y_{lm}}{\sin\theta \partial\phi} \right) \hat{\theta} + \left(-\frac{V^{\phi}_{lm} \partial Y_{lm}}{\partial\theta} \right) \hat{\phi} \tag{66}$$

For this case now,we six independent components of the stress tensor for a particular mode (ℓm) of the velocity are

$$\sigma_{rr} = 0$$

$$\sigma_{r\theta} = im \csc\theta Y_{lm} \left(\frac{-V^{\phi}_{lm}}{r} + \frac{\partial V^{\phi}_{lm}}{\partial r} \right)$$

$$\sigma_{r\phi} = m \cot^2\theta \left(Y_{lm} + e^{i\phi}\sqrt{(\ell-m)(\ell+m+1)} Y_{lm+1} \right) \left(\frac{V^{\phi}_{lm}}{r} - \frac{\partial V^{\phi}_{lm}}{\partial r} \right)$$

$$\sigma_{\theta\phi} = \left(\frac{V^{\phi}_{lm}}{r} \right) \Big(m \left(\cot^2\theta + \csc^2\theta \right) Y_{lm} + 2e^{-i\phi} m \cot\theta \sqrt{(\ell-m)(l+m+1)} Y_{lm+1} + \\ e^{-2i\phi}\sqrt{(\ell-m)(\ell-m-1)(\ell+m+1)(\ell+m+2)} Y_{lm+2}$$

$$\sigma_{\theta\theta} = -2im \csc\theta \left(-(-1+m) \cot\theta Y_{lm} - e^{-i\phi}(l-m)(l+m+1) Y_{lm+1} \right) \frac{V^{\phi}_{lm}}{r}$$

$$\sigma_{\phi\phi} = -2im \csc\theta \left(-(-1+m) \cot\theta Y_{lm} + e^{-i\phi}(l-m)(l+m+1) Y_{lm+1} \right) \frac{V^{\phi}_{lm}}{r}$$

Case II : All A_{lm} are zeros

In this case we have V^{Y}_{lm} and V^{ψ}_{lm} as non-zeros. The Velocity field reduces to the form:

$$\mathbf{V} = \sum_{lm} \left(V^{Y}_{lm} Y_{lm} \right) \hat{r} + \left(V^{\psi}_{lm} \frac{\partial Y_{lm}}{\partial\theta} \right) \hat{\theta} + \left(V^{\psi}_{lm} \frac{\partial Y_{lm}}{\sin\theta \partial\phi} \right) \hat{\phi} \tag{67}$$

For this case,the six independent components of the stress tensora for particular mode (ℓm) of the velocity are

$$\sigma_{rr} = 2Y_{lm}\frac{\partial V^{Y}_{lm}}{\partial r} \tag{68}$$

$$\sigma_{r\theta} = \left(m\cot\theta Y_{lm} + e^{-i\phi}\sqrt{(\ell-m)(l+m+1)}Y_{lm+1}\right)\left(\frac{V^{Y}_{lm} - V^{\psi}_{lm} + r\frac{V^{\psi}_{lm}}{\partial r}}{r}\right) \tag{69}$$

$$\sigma_{r\phi} = im\csc\theta Y_{lm}\left(\frac{V^{Y}_{lm} - V^{\psi}_{lm} + r\frac{\partial V^{\psi}_{lm}}{\partial r}}{r}\right) \tag{70}$$

$$\sigma_{\theta\phi} = \frac{2im\csc\theta}{r}\left((m-1)\cot\theta Y_{lm} + e^{-i\phi}\sqrt{(\ell-m)(l+m+1)}Y_{lm+1}\right)\frac{V^{\psi}_{lm}}{r} \tag{71}$$

$$\sigma_{\theta\theta} = \Big(Y_{lm}V^{Y}_{lm} + \Big(m(m\cot^2\theta - \csc^2\theta Y_{lm} + e^{-i\phi}(1+2m)\cot\theta\sqrt{(\ell-m)(\ell+m+1)}Y_{lm+1} + e^{-i2\phi}\sqrt{(\ell-m)(\ell-m-1)(\ell+m+3)(\ell+m+2)}Y_{lm+2}V^{\psi}_{lm} \tag{72}$$

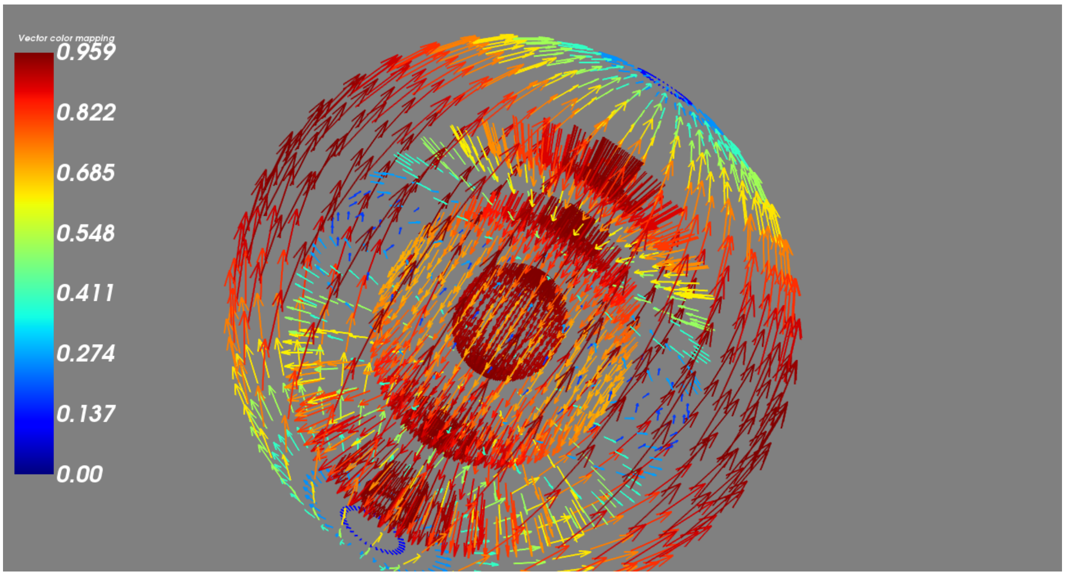
$$\sigma_{\phi\phi} = \frac{2\csc\theta}{r}\big(\sin\theta Y_{lm}V^{Y}_{lm} + (m(\cos\theta\cot\theta - m\csc\theta)Y_{lm} + e^{-i\phi}\cos\theta\sqrt{(\ell-m)(\ell+m+1)}Y_{lm+1}V^{\psi}_{lm} \tag{73}$$

In general,the stress tensor is a sum over all modes when both $\mathbf{C}_{lm}$ and $\mathbf{A}_{lm}$ are non-zero, stress tensor components would be the sum of the respective components as described in the above cases.

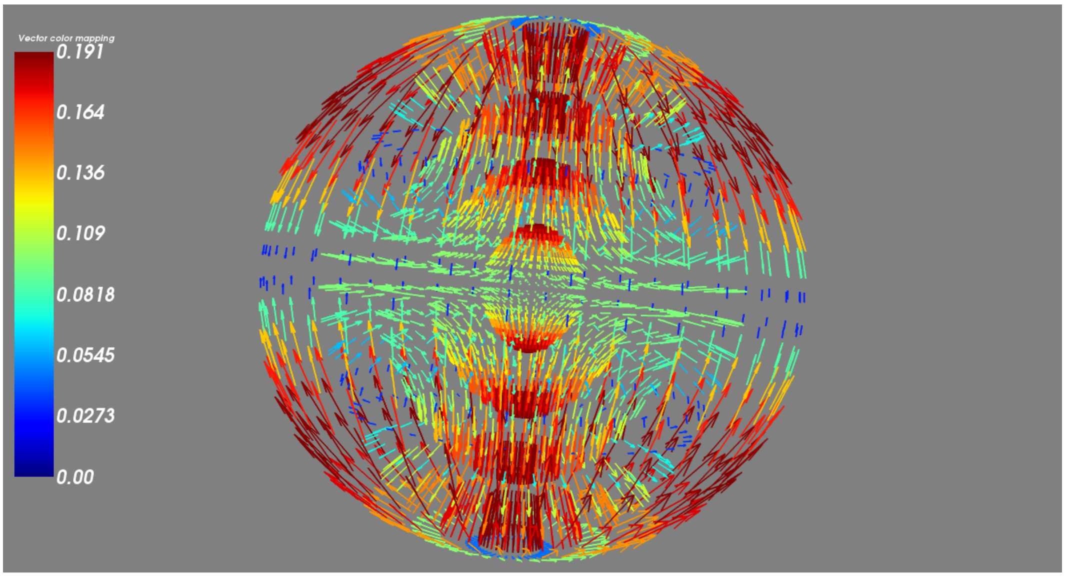
9.Results:Flow patterns calculated and plotted numerically for some special cases:

The above analytical results have been used to compute and visulaize the flows for some cases where the field has a particular form. We use shtns library to calculate the spectral components by taking vector spherical harmonics transform of the surface velocity field specified.

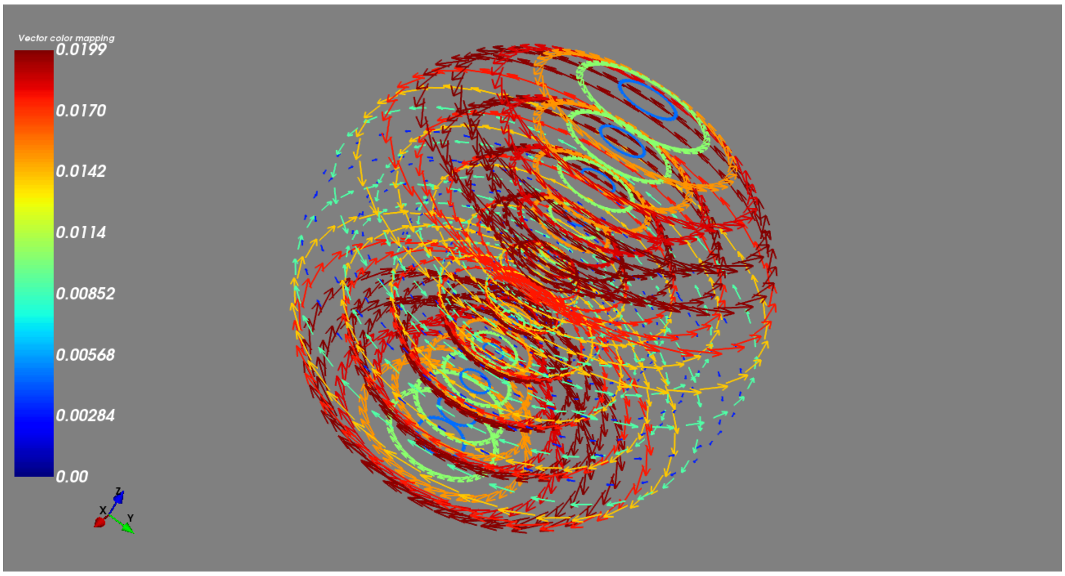
Example I: $V_\theta = \sin\theta$, $V_\phi = 0$



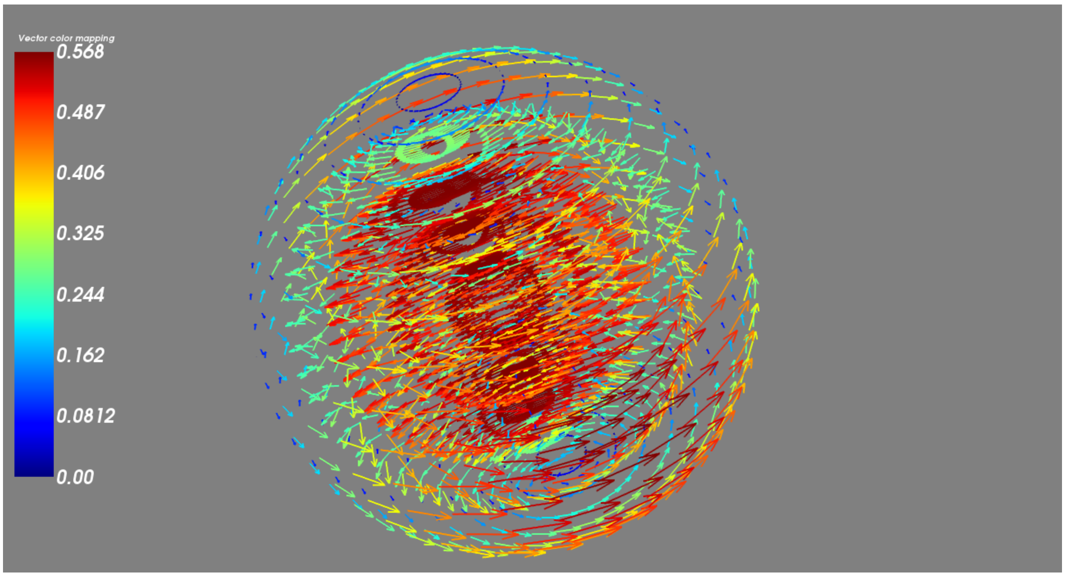
Example II: $V_\theta = \sin\theta\cos\phi$, $V_\phi = 0$



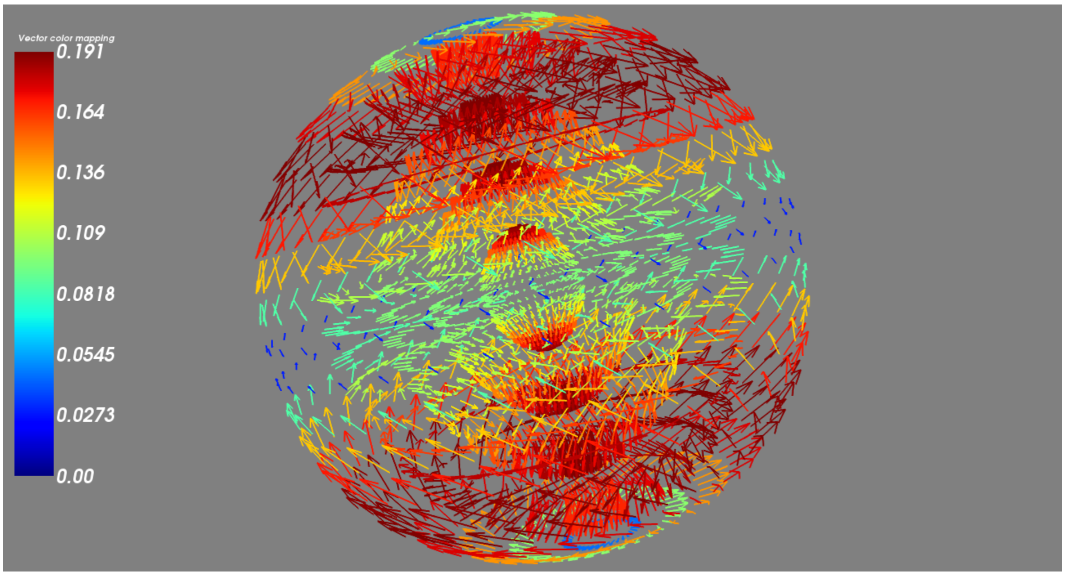
Example III: $V_\phi = \sin\theta\cos\theta$, $V_\theta = 0$



Example IV: $V_\theta = 0$, $V_\phi = \sin\theta\sin\phi$



Example V:$V_\theta = \sin\theta\cos\theta$,$V_\phi = \sin\theta\cos\theta$



In general,we can specify any well defined velocity field on a sphere and can compute corresponding bulk velocity pattern inside the cell.

10.Conclusion

The above bulk velocity and the calculation of stress tensor can be coupled to pattern formation problem on a sphere. The patterns are formed due to coupling of the velocity field and the actomyosin concentration.These surface velocity continuously change which will change the bulk velocity as well.The stress generated by the bulk flows will also couple to the concentration dependent active stress may give rise to new dynamics and results.