The swimming of sperm and other animalcules

B. U. Felderhof, RWTH Aachen

earlier work (1994) with R. B. Jones, QMC, London

„animalcules" = an animal so minute in its size, as not to be the
immediate object of our senses
(Encyclopaedia Britannica, first edition, 1771)
=a microscopic animal
(Mrs. Byrne's Dictionary of Unusual, Obscure,
and Preposterous Words, 1974)
(Concise Oxford Dictionary, 1974)

discovered by
Antonie van Leeuwenhoek, born Oct. 1632, Delft
died Aug. 1723, Delft

cf. Johannes Vermeer, born Oct. 1632, Delft
died Dec. 1675, Delft

Antonie van Leeuwenhoek discovered

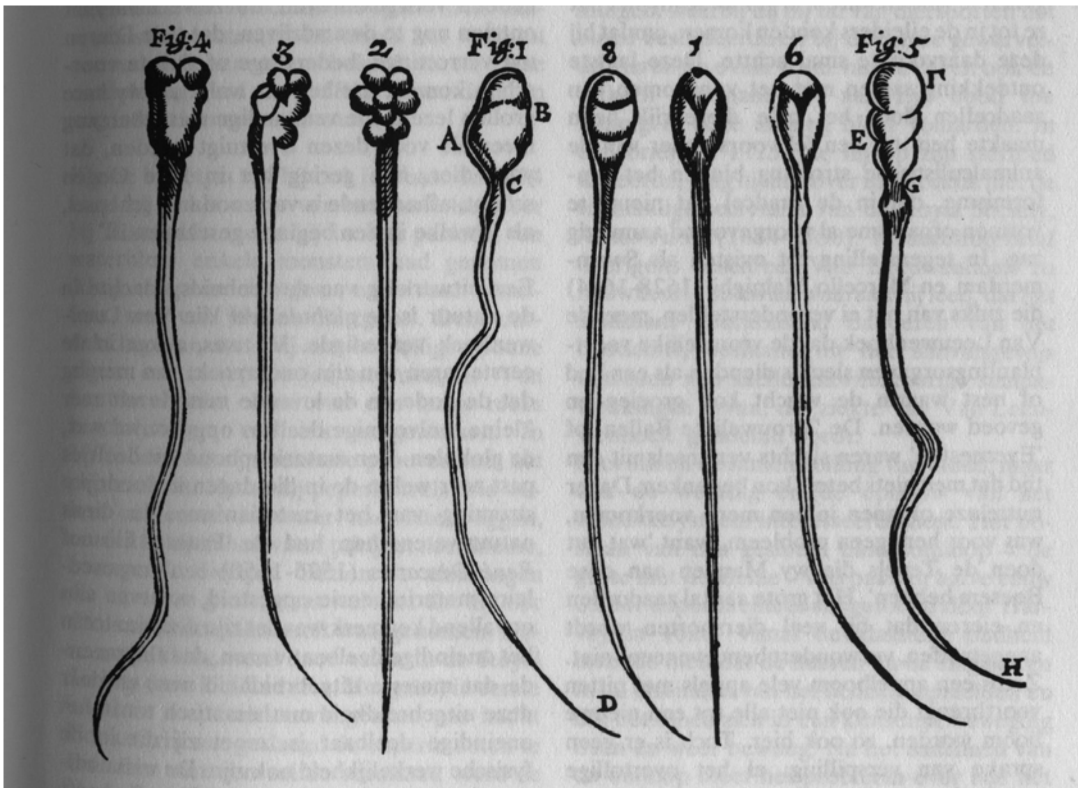
sperm (about 50 microns long)

protozoa (unicellular)
bacteria (about 1 micron)
reproduce by binary fission

many of these microorganisms move in water by swimming

ANTONIUS A LEEUWENHOEK.
Regiæ Societatis Londinensis membrum.

J. Verkolje pinx: *A. de Blois fec*



Zaadcellen; 1-4 mens, 5-8 hond

1-4 van Leeuwenhoek`s sperms

5-8 his dog‘s sperms

In second order perturbation theory one finds steady swimming velocities

$\mathbf{U}_2$ for translation and $\vec{\Omega}_2$ rotation.

Simplification: Low Reynolds number hydrodynamics and point approximation

In low Reynolds number hydrodynamics we can omit the terms

$$\rho \frac{\partial \mathbf{v}}{\partial t} \quad \text{and} \quad \mathbf{v}\cdot\nabla\mathbf{v}$$

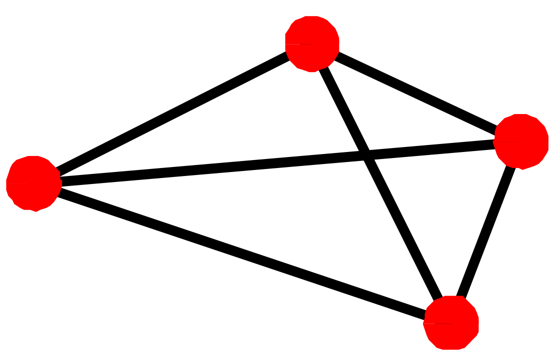
and use the Stokes equations

$$\eta\nabla^2\mathbf{v} - \nabla p = -\mathbf{F} \qquad \nabla\cdot\mathbf{v} = 0$$

In point approximation

$$\mathbf{F} = \sum_{j=1}^{N} \mathbf{K}_j \delta(\mathbf{r} - \mathbf{R}_j)$$

We consider polymer structures consisting of N beads centered at time t at positions $(\mathbf{R}_1(t), \ldots, \mathbf{R}_N(t))$



Forces $\{\mathbf{K}_j(t)\}$ periodic in time with period T

Since the equations do not involve a time derivative the forces determine fluid velocity and pressure instantaneously at any time t.

Fluid velocity

$$\mathbf{v}(\mathbf{r}) = \sum_{j=1}^{N} \mathbf{T}(\mathbf{r} - \mathbf{R}_j) \cdot \mathbf{K}_j$$

with Oseen tensor

$$\mathbf{T}(\mathbf{r}) = \frac{1}{8\pi\eta} \frac{\mathbf{1} + \hat{\mathbf{r}}\hat{\mathbf{r}}}{r}$$

The instantaneous particle velocities are

$$\mathbf{u}_j = \mu_j \mathbf{K}_j + \sum_{k \neq j}^{N} \mathbf{T}(\mathbf{R}_j - \mathbf{R}_k) \cdot \mathbf{K}_k \qquad (j = 1, ..., N)$$

μ_j mobility of bead j $\qquad \mu_j = \frac{1}{6\pi\eta a_j}$

Stokesian dynamics: $\frac{d\mathbf{R}_j}{dt} = \mathbf{u}_j(\mathbf{R}_1(t), ..., \mathbf{R}_N(t)) \qquad (j = 1, ..., N)$

The total force is required to vanish

$$\sum_{j=1}^{N} \mathbf{K}_j = 0$$

We write the bead positions as a sum of two terms

$$\mathbf{R}_j(t) = \mathbf{S}_j(t) + \xi_j(t)$$

where the positions $\{\mathbf{S}_j(t)\}$ describe the mean swimming motion with constant translational velocity $\mathbf{U}$ and rotational velocity $\vec{\Omega}$

The positions $\{\mathbf{S}_j(t)\}$ are solutions of the equations of motion

$$\frac{d\mathbf{S}_j(t)}{dt} = \mathbf{U} + \vec{\Omega} \times (\mathbf{S}_j(t) - \mathbf{C}(t)) \qquad (j = 1, ..., N)$$

with initial positions $\{\mathbf{S}_{0j} = \mathbf{S}_j(0)\}$ centered at

$$\mathbf{C}_0 = \sum_{j=1}^{N} a_j \mathbf{S}_{0j} / \sum_{j=1}^{N} a_j$$

The center of resistance $\mathbf{C}(t)$ moves with constant velocity $\mathbf{U}$

$$\mathbf{C}(t) = \mathbf{C}_0 + \mathbf{U}t$$

We require that the displacements $\{\xi_j(t)\}$ are periodic in time, and that their average over a period vanishes

$$\langle \xi_j \rangle = \frac{1}{T}\int_0^T \xi_j(t)\,dt = 0 \qquad (j = 1,\ldots,N)$$

To first order in the forces $\mathbf{K}_1,\ldots,\mathbf{K}_N$ the particle velocities are given by

$$\mathbf{u}_j^{(1)}(t) = \sum_{k=1}^{N} \mu_{jk} \cdot \mathbf{K}_k(t)$$

where $\{\mu_{jk}\}$ is the mobility matrix for the static structure $(\mathbf{S}_{01},\ldots,\mathbf{S}_{0N})$

By integration over time $\xi_j(t) = \int^t \mathbf{u}_j^{(1)}(t')\,dt'$

Because of the displacements of the beads there is a second order correction to their velocities given by

$$\delta u_{j\alpha}^{(2)}(t) = \sum_{k \neq j}^{N} \xi_{j\beta}^{(1)}(t) G_{\beta\alpha\gamma}(\mathbf{S}_{0j} - \mathbf{S}_{0k}) K_{k\gamma}(t) \qquad (j = 1,\ldots,N)$$

where $\mathbf{G}(\mathbf{r})$ is the third rank tensor $\mathbf{G}(\mathbf{r}) = -\frac{\partial}{\partial \mathbf{r}}\mathbf{T}(\mathbf{r})$

The corresponding second order flow field $\delta\mathbf{v}^{(2)}(\mathbf{r},t)$ can be viewed as being generated by induced forces $\{\delta\mathbf{F}_j^{(2)}(t)\}$ that can be calculated from

$$\delta\mathbf{F}_j^{(2)}(t) = \sum_{k=1}^{N} \zeta_{jk} \cdot \delta\mathbf{u}_k^{(2)}(t)$$

Since there is no flow of momentum or angular momentum to infinity, the polymer must move as a whole such that the actual second order bead velocities are

$$\mathbf{u}_j^{(2)}(t) = \mathbf{u}^{(2)}(t) + \vec{\omega}^{(2)}(t) \times (\mathbf{S}_{0j} - \mathbf{C}_0) + \delta\mathbf{u}_j^{(2)}(t) \qquad (j = 1,\ldots,N)$$

with velocities $\mathbf{u}^{(2)}(t)$ and $\vec{\omega}^{(2)}(t)$ such that the total induced force and torque vanish.

On time average this implies that the swimming velocities

$$\mathbf{U}^{(2)} = \left\langle \mathbf{u}^{(2)}(t) \right\rangle \qquad \vec{\Omega}^{(2)} = \left\langle \vec{\omega}^{(2)}(t) \right\rangle$$

are given by

$$\mathbf{U}^{(2)} = \overleftrightarrow{\mu}^{tt} \cdot \mathbf{F}^{St} + \overleftrightarrow{\mu}^{tr} \cdot \mathbf{T}^{St}$$

$$\vec{\Omega}^{(2)} = \overleftrightarrow{\mu}^{rt} \cdot \mathbf{F}^{St} + \overleftrightarrow{\mu}^{rr} \cdot \mathbf{T}^{St}$$

with Stokes force and torque

$$\mathbf{F}^{St} = -\sum_{j=1}^{N} \left\langle \delta \mathbf{F}_j^{(2)} \right\rangle \qquad \mathbf{T}^{St} = -\sum_{j=1}^{N} ((\mathbf{S}_{0j} - \mathbf{C}_0) \times \left\langle \delta \mathbf{F}_j^{(2)} \right\rangle)$$

The rate at which energy is dissipated equals

$$D(t) = \sum_{j=1}^{N} \mathbf{K}_j(t) \cdot \mathbf{u}_j(t)$$

To second order in the forces $\qquad D^{(2)}(t) = \sum_{j=1}^{N} \mathbf{K}_j(t) \cdot \mathbf{u}_j^{(1)}(t)$

Average over a period $\qquad \left\langle D^{(2)}(t) \right\rangle = \left\langle \sum_{j=1}^{N} \mathbf{K}_j(t) \cdot \mathbf{u}_j^{(1)}(t) \right\rangle$

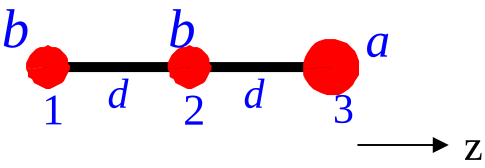
Define dimensionless efficiencies of swimming as the ratios

$$E_T(\omega) = \eta \omega L^2 \frac{\left| \mathbf{U}^{(2)} \right|}{\left\langle D^{(2)} \right\rangle} \qquad E_R(\omega) = \eta \omega L^3 \frac{\left| \vec{\Omega}^{(2)} \right|}{\left\langle D^{(2)} \right\rangle}$$

where L is the size of the polymer.

Then one can compare efficiencies of different strokes.

Longitudinal mode for structure



Forces $\mathbf{K}_1(t), \mathbf{K}_2(t) \parallel \mathbf{e}_z, \quad \mathbf{K}_3(t) = -\mathbf{K}_1(t) - \mathbf{K}_2(t)$

All motion along z-direction.

$$K_1(t) = A\sin\omega t$$
$$K_2(t) = A\sin(\omega t + \alpha)$$
$$K_3(t) = -K_1(t) - K_2(t)$$

Optimal motion in +z-direction for $\alpha \approx -\frac{2\pi}{3}$

$$u_{1z}^{(1)} = \frac{1}{24\pi\eta bd}\left[(4d-3b)K_1 + 3bK_2\right]$$

$$u_{2z}^{(1)} = \frac{1}{12\pi\eta bd}(2d-3b)K_2$$

$$u_{3z}^{(1)} = \frac{-1}{24\pi\eta bd}\left[(4d-3a)K_1 + (4d-6a)K_2\right]$$

$$\delta u_{1z}^{(2)} = \frac{1}{16\pi\eta d^2}\left[(\xi_{1z}-\xi_{3z})K_1 - (3\xi_{1z} - 4\xi_{2z} + \xi_{3z})K_2\right]$$

$$\delta u_{2z}^{(2)} = \frac{1}{4\pi\eta d^2}\left[(-\xi_{1z} + 2\xi_{2z} - 3\xi_{3z})K_1 + (\xi_{2z} - \xi_{3z})K_2\right]$$

$$\delta u_{3z}^{(2)} = \frac{1}{16\pi\eta d^2}\left[(-\xi_{1z} + \xi_{3z})K_1 - 4(\xi_{2z} - \xi_{3z})K_2\right]$$

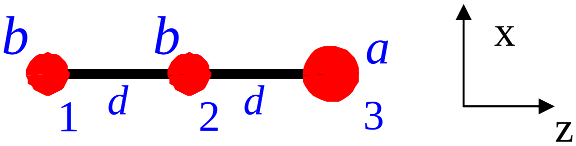
$$U^{(2)} = \frac{-A^2\sin\alpha}{192\pi^2\eta^2 d^3\omega}\,\frac{4d(56d^2 - 174bd + 135b^2) - 3a(88d^2 - 270bd + 189b^2)}{16bd(2d-3b) + a(16d^2 - 72bd + 63b^2)}$$

$$\Omega^{(2)} = 0$$

$$\left\langle D^{(2)} \right\rangle = \frac{A^2}{24\pi\eta abd}\left[4(a+b)d - 9ab + b(4d-3a)\cos\alpha\right]$$

$$\alpha_0 = -\arccos\frac{b(4d-3a)}{4(a+b)d - 9ab}$$

Transverse mode for structure



Forces $\mathbf{K}_1(t), \mathbf{K}_2(t) \parallel \mathbf{e}_x, \quad \mathbf{K}_3(t) = -\mathbf{K}_1(t) - \mathbf{K}_2(t)$

First order motion along x-direction.

$$K_1(t) = A\sin\omega t$$
$$K_2(t) = A\sin(\omega t + \alpha)$$
$$K_3(t) = -K_1(t) - K_2(t)$$

Optimal motion in +z-direction for $\alpha \approx \dfrac{2\pi}{3}$

$$u_{1x}^{(1)} = \frac{1}{48\pi\eta bd}\left[(8d-3b)K_1 + 3bK_2\right]$$

$$u_{2x}^{(1)} = \frac{1}{24\pi\eta bd}(4d-3b)K_2$$

$$u_{3x}^{(1)} = \frac{-1}{48\pi\eta ad}\left[(8d-3a)K_1 + (8d-6a)K_2\right]$$

$$\delta u_{1z}^{(2)} = \frac{1}{32\pi\eta d^2}\left[(-\xi_{1x}+\xi_{3x})K_1 + (3\xi_{1x}-4\xi_{2x}+\xi_{3x})K_2\right]$$

$$\delta u_{2z}^{(2)} = \frac{1}{8\pi\eta d^2}\left[(\xi_{1x}-2\xi_{2x}+3\xi_{3x})K_1 - (\xi_{2x}-\xi_{3x})K_2\right]$$

$$\delta u_{3z}^{(2)} = \frac{1}{32\pi\eta d^2}\left[(\xi_{1x}-\xi_{3x})K_1 + 4(\xi_{2x}-\xi_{3x})K_2\right]$$

$$U^{(2)} = \frac{A^2\sin\alpha}{768\pi^2\eta^2 d^3\omega}\,\frac{2d(224d^2-534bd+297b^2)-3a(164d^2-360bd+189b^2)}{16bd(2d-3b)+a(16d^2-72bd+63b^2)}$$

$$\Omega^{(2)} = 0$$

$$\left\langle D^{(2)}\right\rangle = \frac{A^2}{48\pi\eta abd}\left[8(a+b)d - 9ab + b(8d-3a)\cos\alpha\right]$$

$$\alpha_0 = \arccos\frac{b(8d-3a)}{8(a+b)d-9ab}$$

Similarly for longer linear chains.

Sperm can be modelled as a head of radius a followed by a tail of beads of radius b.

Instead of specifying N periodic forces one can start by specifying N−1 first order displacements and calculate the forces and the N-th displacement from

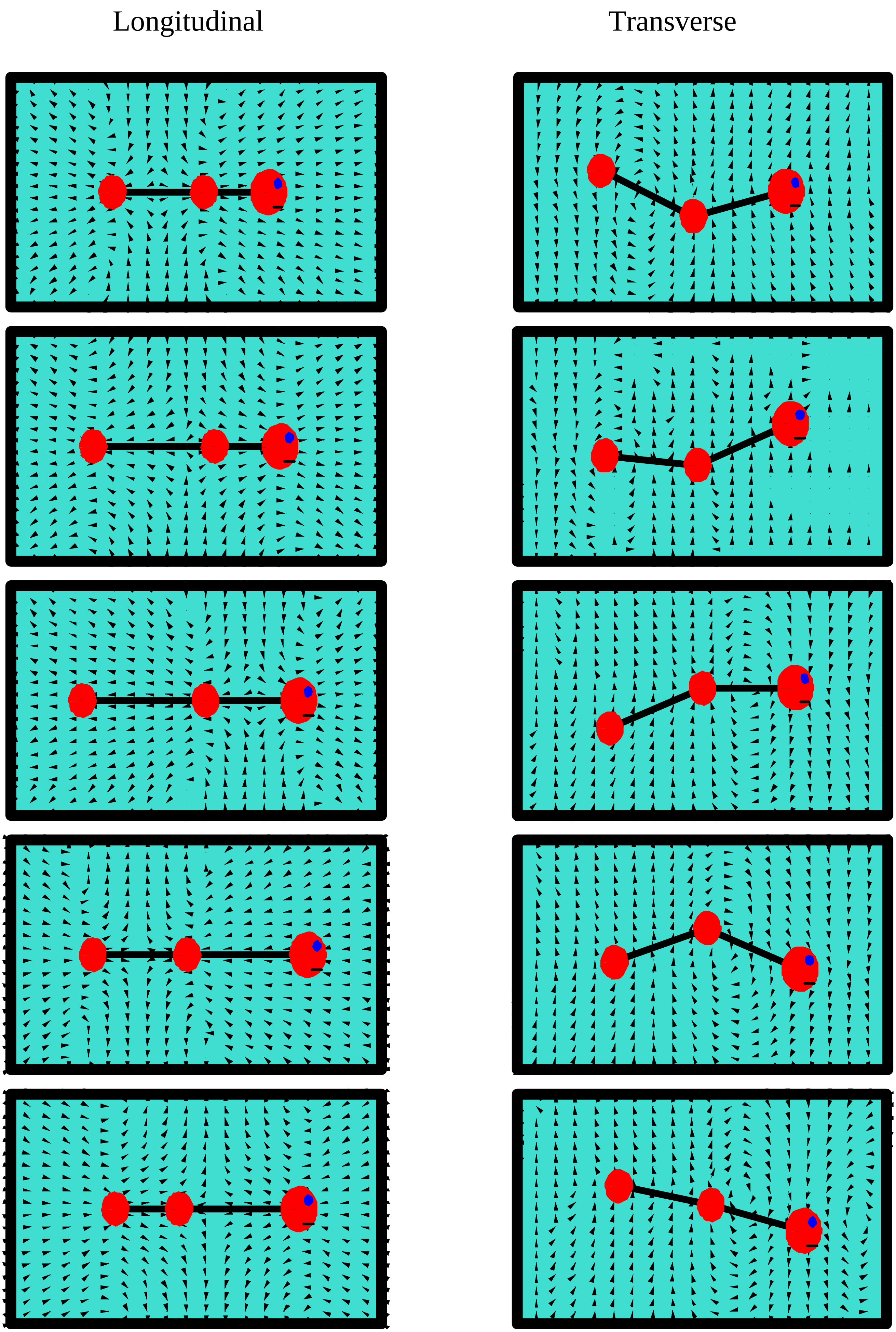
$$K_j(t) = \sum_{k=1}^{N} \zeta_{jk} u_k^{(1)}(t) \quad \text{and} \quad \sum_{j=1}^{N} K_j(t) = 0$$

In 3D situations one can specify N−2 displacement vectors and calculate forces and the last two displacements from the friction matrix and the condition that total force and torque vanish.

For a body one can specify shapes S_0 and S(t).
Such calculations were performed in
B.U. Felderhof and R. B. Jones, Physica A 202, 94 (1994)

We also considered effect of inertial terms $\rho \frac{\partial \mathbf{v}}{\partial t}$ and $\rho \mathbf{v} \cdot \nabla \mathbf{v}$

The special case of S_0= sphere was studied in
B.U. Felderhof and R. B. Jones, Physica A 202, 119 (1994)


Longitudinal
Transverse

MOVIE1