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# Charge effects on phospholipid monolayers in relation to cell motility

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**It is shown that the interfacial free energy of adsorbed phospholipid layers is dependent on the interfacial inner potential difference and on the local pH at the surface. Gradients of potential and pH result in the onset of Marangoni hydrodynamic convective fluxes at the phase adjoining a phospholipid monolayer. It is proposed that the coupling between potential, pH and interfacial Gibbs energy can provide an elementary driving force for cell and organelle motility, phagocytosis and streaming effects. It is shown that the order of magnitude of the surface shear stress generated by surface tension gradients is sufficient to account for cytoplasmic streaming in cells.**

## Introduction

Motility phenomena in living cells has attracted a great deal of attention since the microscopical observation of protozoa by Leewenhoeck ** [1], over 3 centuries ago. Indeed, self-generated movement has been considered an essential attribute of life. The basic mechanisms responsible for motility and streaming in non-muscular cells are not clearly understood. These have been discussed lately mainly in terms of actin-myosin interaction [2–4]. In this biochemical approach to cytodynamics, hydrodynamic and interfacial mechanical aspects are usually not considered and it is generally accepted that cytoplasm movement is based on contractility [5]. However, these mechanisms, which are based on the existence of a cytoskeleton, do not provide a simple explanation for movement involving the recognition of directionality as observed in amoebiodal movements, such as in phagocytosis. Short-range electrostatic forces are clearly important in this context for the sensing of fields located outside the cell; phagocytic response is triggered by organisms or substances carrying a positive charge [6] which points to electrostatic effects at the membrane level being responsible for the early events in phagocytosis. However, recognition at distances greater than the Debye screening length are common [7], indicating that chemotaxis involves the sensing by the cell membrane of gradients of concentration of specific chemicals, which are able to trigger a directional movement. It can be said that the biochemical approach to cell motility explains how the cellular engine works, and the purpose of this paper is to show that the cell membrane can represent the driving element of the cell as it senses the direction and controls the speed by always minimizing its Gibbs free energy.

The study of the physicochemical basis of these sensing-motility phenomena is not easy, although it is of relevance to the understanding of im-

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portant problems such as immunological response, cell growth and division, phagocytosis, pinocytosis, etc. In this respect, a simple model system composed of half a phospholipid bilayer can be used conveniently for the analysis of the contribution of the cell membrane to cytokinetic phenomena in the living cell. In the present work, the coupling between the interfacial Gibbs free energy of a lipid layer, represented by the interfacial tension, with chemical and electrical potentials is examined. This coupling, equivalent to the sensing by the phospholipid molecules of the electrical inner potential difference across the membrane, results in the generation of hydrodynamic motions which can be associated with cytokinetic phenomena.

The interfacial Gibbs energy of a phospholipid layer is an accessible quantity which is seldom discussed in relation to cell or organelle motility and although it is not readily accessible for whole cells, it can be measured in model systems [8,9]. The present study is based on recent developments in the investigation of the interface between two immiscible electrolyte solutions, across which controlled differences in inner potentials (also called Galvani potential) can be applied.

## Electrochemistry of liquid/liquid interfaces

In 1973, Gavach [10] showed that the interface between two immiscible electrolyte solutions (ITIES) could be polarised in the same way as an electrode/electrolyte interface, if the electrolytes chosen were hydrophilic and hydrophobic for the aqueous and non-aqueous phases, respectively (e.g., NaCl in water/tetrabutylammonium tetraphenylborate ($TBA^+$-$TPB^-$) in a polar organic solvent). Further work has shown that standard electrochemical methodology can be used to investigate this new type of polarisable interfaces. Using a thermodynamic approach, the structure of the liquid/liquid interface has been studied [11–13] and it appears that the interface can be regarded as composed of a thin mixed solvent layer that ions from both phases can partially penetrate. Interfacial tension and capacitance measurements have furthermore clearly indicated that the inner electrical potential varies in a continuous way from the bulk of the aqueous phase to the bulk of the non-aqueous phase across the two back-to-back diffuse double layers. It has been recently shown that this continuous inner potential profile can be simulated from the Gouy-Chapman theory and in this way the inner potential in the interfacial region can be estimated [14].

The thermodynamic analysis of the ITIES shows that the Lippmann equation used for the polarised mercury/electrolyte interface is also valid in the case of a liquid/liquid interface [13]:

$$-\left(\frac{\partial \gamma}{\partial \Delta E}\right)_{T,P,\mu_i} = Q \tag{1}$$

where $\gamma$ is the interfacial tension, $\Delta E$ the potential difference between two reference electrodes each reversible to an ion in each phase [13]. $Q$ is the interfacial charge density defined as the difference between the number of organic cations and anions in the interfacial region, equivalent to the difference in the number of hydrophilic anions and cations. At constant $T$, $P$ and composition, any change in potential between the reference electrodes equals the change in inner potential difference between the two bulk phases (vide infra) and therefore Eqn. 1 becomes:

$$-\left(\frac{\partial \gamma}{\partial \Delta_\alpha^\beta \phi}\right)_{T,P,\mu_i} = Q \tag{2}$$

where $\Delta_\alpha^\beta \phi$ is the inner potential difference $\phi^\beta - \phi^\alpha$ between the two bulk phases $\alpha$ and $\beta$. Although the inner potential difference is not a measurable quantity, its value can be estimated using some extra-thermodynamic assumptions. At liquid/liquid interfaces, the equality of the Gibbs energy of transfer of two ions of the same size but carrying opposite charges such as tetraphenylarsonium and tetraphenylborate is usually assumed for establishing an ionic scale of Gibbs energies of transfer. Besides this assumption, an extended form of the Debye-Huckel theory or the equality of the activity of both ions is used for the estimation of individual ionic activities. Values of $\Delta_\alpha^\beta \phi$ based on the above convention can therefore be calculated with an accuracy which will be dependent on the applicability of the ionic activity theory employed to the particular experimental conditions.

Consequently, liquid/liquid interfaces are ideally suited to monitor the behaviour of amphiphilic molecules in an environment where the electrical inner potential can be controlled. Indeed, these interfaces have been used as a model for cell membranes, since the surface chemistry and the electrochemistry of such simple membrane analogues are well-defined. Previous work on interfacial tension measurements at a liquid/liquid interface in the presence of adsorbed phospholipids has shown that it is possible to monitor the state of charge of the polar moiety as a function of both local pH or electrical inner potential [9].

## Experimental

Interfacial tension measurements have been used in this work to study the adsorption of phospholipids as a function of the inner potential differences across a polarised liquid/liquid interface. These measurements have been carried out on a hanging electrolyte drop electrode by the technique of the inflexion plane using a video profile digitiser (Dydropp, U.K.) [15]. The interface was polarised using a four-electrode potentiostat and the applied potential refers to the cell:

$$\underset{E_1}{\text{Hg}\,|\,\text{HgCl}\,|\,\text{KCl saturated}\,|\,\text{0.01 M KCl in water I}\,|\,\text{0.001 M TBA}^+\text{TPB}^-\text{ in 1,2-DCE}\,|\,\text{0.01 M TBA}^+\text{Cl}^-\text{ in water II}\,|\,\text{KCl saturated}\,|\,\text{HgCl}\,|\,\text{Hg}}_{E_2}$$

where $TBA^+TPB^-$ and $TBA^+Cl^-$ represent tetrabutylammonium tetraphenylborate and tetrabutylammonium chloride, respectively, and 1,2-DCE represents 1,2-dichloroethane. The Galvani potential difference between the aqueous solution (0.01 M KCl) and the non-aqueous solution (0.001 M $TBA^+TPB^-$) is related to the applied potential difference by:

$$\Delta^{DCE}_{H_2O}\phi = (E_2 - E_1) - \frac{1}{F}\Delta G^{o,H_2O\rightarrow DCE}_{t,TBA^+} - \frac{RT}{F}\ln\frac{a^{DCE}_{TBA^+}}{a^{H_2O(II)}_{TBA^+}} \quad (3)$$

where $\Delta^{DCE}_{H_2O}\phi$ is the inner potential difference between the organic and aqueous phases, $\Delta G^{o,H_2O\rightarrow DCE}_{t,TBA^+}$ is the standard Gibbs energy of transfer of $TBA^+$ from water to 1,2-dichloroethane and $a^{i}_{TBA^+}$ represents the ionic activity of the $TBA^+$ cation in solvent $i$. Eqn. 3 is obtained assuming that the two liquid junction potentials of the saturated calomel electrodes are the same.

Although the last two terms of Eqn. 3 are not amenable to measurement, it is possible to estimate them as previously discussed. Using the data of Czapkiewicz and Czapkiewicz-Tutaj ($\Delta G^{o,H_2O\rightarrow DCE}_{t,TBA^+} = -21.8$ kJ·mol$^{-1}$) [16], and a value of the association constant of $TBA^+TPB^-$ in 1,2-dichloroethane of $K_A = 0.171 \cdot 10^{-4}$ [17], the inner potential difference is given by:

$$\Delta^{DCE}_{H_2O}\phi = (E_2 - E_1) + 0.310 \text{ (in V)} \quad (4)$$

The cell employed and the experimental details have been published elsewhere [13]. The temperature was kept constant at 25°C using a circulating thermostatic bath.

Chromatographically pure grade I egg-yolk phosphatidylcholine (PC) (Lipid Products, Surrey, U.K.), was used without further purification. A 1 mM stock solution was prepared by evaporation under vacuum of the methanol/chloroform original mixture and by dissolution in AnalaR 1,2-dichloroethane (B.D.H., U.K.). The stock solutions were kept at −20°C.

The mechanical effects of applied potential differences across a polarised interface with adsorbed phospholipid were studied by measuring the rate of displacement of droplets of solutions of phosphatidylcholine (PC) in 1,2-dichloroethane immersed in an aqueous solution under the influence of a gradient of potential. For these studies, the system was composed of 10 mM KCl/1 mM citric acid/10 μM sodium tetraphenylborate ($Na^+TPB^-$) in water, and of 1 mM $TBA^+TPB^-$/25 μM PC in 1,2-dichloroethane. $Na^+TPB^-$ was used as a potential determining ion to fix the average potential of the droplet in the potential region of the electrocapillary curve when the potential and

pH dependence of the interfacial tension is the greatest (see later, Fig. 1).

The mobility experiments were carried out by placing an organic droplet of approx. 4 mm in diameter in a glass trough. An homogeneous electric field of 2 $V \cdot cm^{-1}$ was applied by passing an electric current through the aqueous phase using two platinum gauze electrodes placed at both ends of the trough. The rate of displacement of the droplets was measured by digital recording of the drop coordinates at different times using the video profile digitiser.

## Results

Fig. 1 shows the potential dependence of the interfacial tension at the 1,2-dichloroethane/water interface in the presence and absence of PC in the non-aqueous phase, for two different pH values. The top curve represents the classical behaviour of a polarised liquid/liquid interface in the absence of adsorption [12,13]. From Eqn. 2, it follows that the maximum in $\gamma$ represents the potential at which the interfacial charge is zero. The two bottom curves represent the interfacial Gibbs energy when phospholipid molecules are adsorbed at two different bulk pH values. As can be seen, two different regions of potential characterise the properties of adsorbed PC. For positive potentials, i.e., when $\Delta^{DCE}_{H_2O}\phi > 0$, and for a pH of 5, the value of the interfacial charge is negligible, as shown by the independence of the interfacial tension with potential. It can be concluded, therefore, that in this potential range the polar head of the phospholipid is in the zwitterionic form [8,9]. As expected, this potential range is extended for neutral pH values.

The increase of interfacial tension as the potential is made more negative indicates a net positive organic surface charge (Eqn. 2). The changes in interfacial charge are due to the dependence on potential of the degree of protonation of the phosphate group in the polar moiety of the adsorbed phospholipid [9], and consequently the phospholipid behaves as a cationic surfactant when the aqueous phase is made positive with respect to the oil phase. When the pH of the solution is near neutrality, the polar head is in the zwitterionic form, and the potential range where $Q$ is negligible is increased. Therefore, the protonation of the phosphate group of monolayers of phospholipids adsorbed at liquid/liquid interfaces is both pH- and potential-dependent.

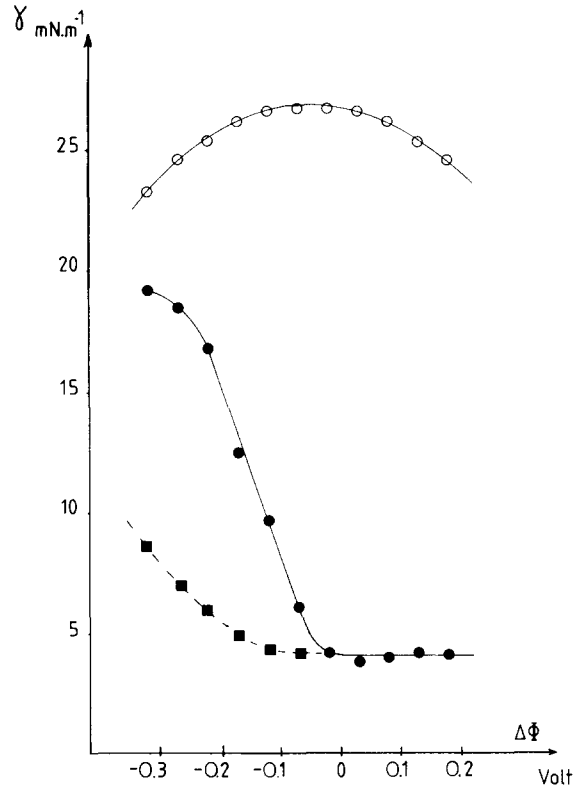


Fig. 1. Potential dependence of the interfacial tension of the 1,2-dichloroethane/water interface for solutions containing: (○) 0.01 M KCl in water (pH 5) and $10^{-3}$ M tetrabutylammonium tetraphenylborate in 1,2-dichloroethane; (●) idem after the addition of phosphatidylcholine (Lipid Products, Surrey) to a concentration of 25 $\mu$M, and (■) idem at pH 6.8 for an aqueous phase composition of 0.01 M $KCl/Na_2HPO_4$. $\Delta\phi$ represents the inner potential difference between the oil and aqueous phase and these values have been calculated from measured potential differences (Eqn. 3).

## Discussion

*Marangoni effects at phospholipid layers*

An important consequence of the unusual potential and pH dependence of the interfacial tension of adsorbed monolayers of phospholipids is the possibility of inducing large changes in interfacial Gibbs energy by altering either the

potential or the pH at the interface. It is precisely this remarkable property of phospholipid layers that allows a coupling between surface movement, pH and potential. If the interfacial tension of a liquid/liquid system is not uniform due to the presence of irreversible reactions occurring with different rates in different regions of its interface, streaming effects and bulk motility are observed [18]. (See Ref. 19 for a review on the hydrodynamic aspects of this problem). This is the well-known Marangoni effect which results in the generations of hydrodynamic fluxes in the presence of surface tension gradients. These fluxes result from the difference in Gibbs energy of solvent molecules located in the vicinity of the interface in regions of different interfacial tension. In this way, molecules present in regions of low interfacial tension will be dragged to regions of high interfacial tension by the imbalance of surface forces for the system to minimise its Gibbs energy.

Surface-tension-driven instabilities at the liquid/vapour interface were originally observed for liquids with an imposed temperature gradient [20]. It has been demonstrated that surface forces rather than buoyancy effects [21] are entirely responsible for these induced convective fluxes. In relation to the discussion that follows, it must be stressed that these effects are not restricted to any particular type of interface, as long as a surface or interfacial tension gradient is present, i.e., gradient of interfacial Gibbs energy is maintained by external means [20].

For a phospholipid layer, a driving force for irreversible subjacent liquid motion can be generated by a surface tension gradient supported by a pH or potential gradient, or both. As can be seen in Fig. 1, a change in interfacial potential of 50 mV will result in a surface tension change of 3.5 $mM \cdot m^{-1}$ at an applied potential of approx. $-0.15$ V for the system studied. A similar change in surface tension can be produced at this potential by a variation in the pH of approx. 1 unit, showing that pH and potential are interconvertible variables from the point of view of the interfacial driving force for charge-induced movement at the interface between a monolayer of phospholipids and the solution. It is important to recognise in this respect, that the onset of the Marangoni instability does not require the motion of the lipid layer itself, but rather that of the adjoining liquid. Neither these effects are dependent on the presence of a liquid/liquid system and will equally well occur at a solid/liquid interface, since the only requirement is the setting of a gradient of Gibbs energy at the interface, and the function of the lipid is just to generate an interfacial tension gradient.

A simple way of testing these ideas was to study the macroscopic movements of uncharged oil droplets containing phospholipid and immersed in an electrolyte solution, through which an electric field was applied. In acidic solutions (Fig. 1), a large difference of surface tension can be induced by imposing a potential difference in

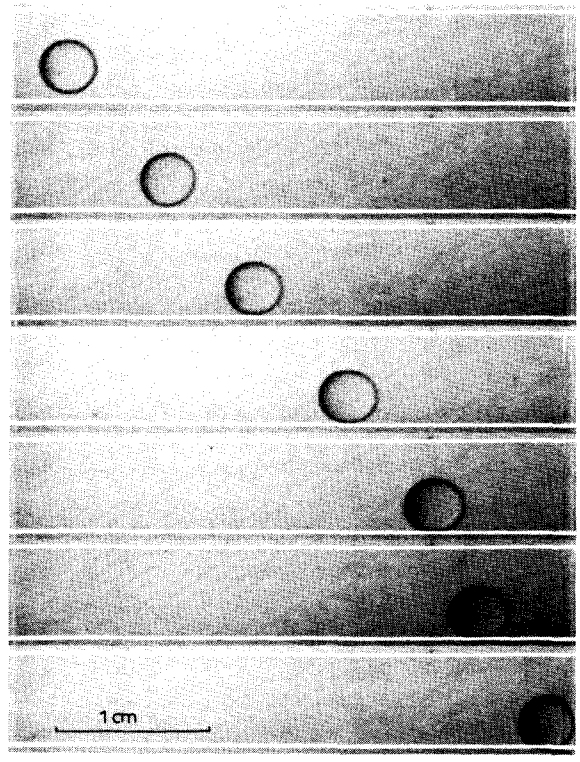


Fig. 2. Movement of a droplet of 1,2-dichloroethane-containing phosphatidylcholine in an aqueous acidic solution. The speed of the droplet moving at the bottom of the trough was about 1.2 $cm \cdot min^{-1}$. The time lapsed between photographs is of 30 s, and the direction of movement is from left to right. The terminal velocity is determined by rheological factors at the oil/glass interface, giving rise to uneven velocities. Oil composition = 1 mM $TBA^+TPB^-$/25 $\mu$M phosphatidylcholine; aqueous phase = 10 $\mu$M KCl/1 mM citric acid/10 $\mu$M $Na^+TPB^-$.

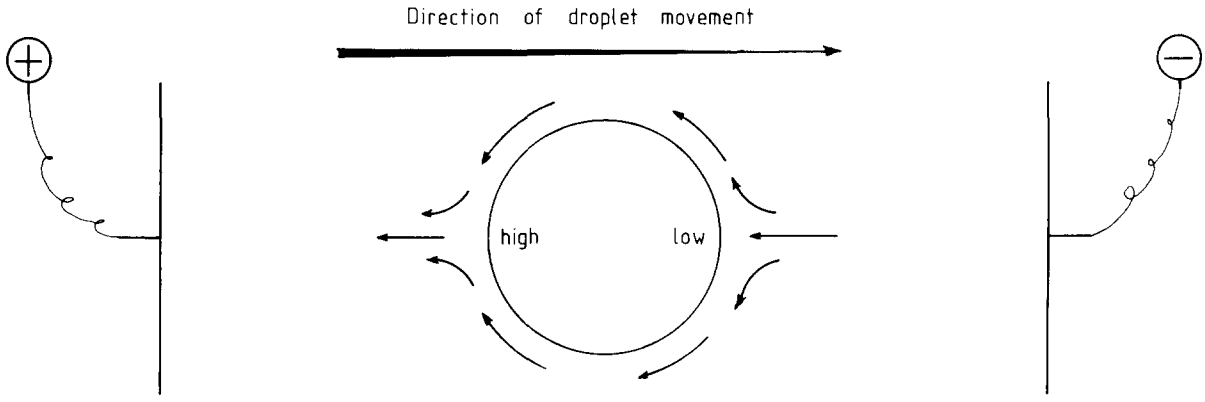


Fig. 3. Schematic drawing of the Marangoni streaming in the aqueous phase caused by the surface tension gradient due to a potential difference between different parts of a droplet.

the solution surrounding the drop. For instance, the interface facing the positive electrode will have a negative inner potential difference (oil – water), and hence, the interfacial tension in this region will have a high value. The opposite effect will occur on the side of the drop facing the negative electrode. The large interfacial tension gradient thus generated, results in a rapid translational movement of the droplet, as shown in Fig. 2, and Fig. 3 shows schematically the expected Marangoni streaming. The direction of movement was, as expected, toward the region of low surface tension, i.e., towards the negative electrode, in agreement with the mathematical modelling of the Marangoni effect at spherical droplets developed by Sorensen [20]. The direction of motion was reversed on changing the field direction.

When the experiment described in Fig. 2 was repeated without the addition of PC, no motion was observed, showing that the motility of the droplet reflects the coupling between surface tension of adsorbed monolayers and the local electrical potential, and is not due to an electrophoretic effect. These changes are not due to desorption of the PC monolayer when the oil is made negative with respect to water, as shown by recent work on the potential dependence of surface excesses to be published elsewhere. The main reason for the change in interfacial tension observed in Fig. 1, is the protonation of the adsorbed layer, and no desorption process needs to be invoked to account for the very sharp changes in interfacial tension observed. The only requirement to obtain surface tension gradients in our experiments is to have different parts of the lipid layer in different states of ionisation and this effect is a consequence of the applied potential difference. It is proposed therefore, that the changes of interfacial potential across the PC monolayer alters the surface ionization of the polar moeity of the phospholipid [9,23], resulting in localized changes in interfacial tension.

*Potential- and pH-driven Marangoni effect and cell motility*

It is proposed that the coupling between interfacial ionisation of cell membrane phospholipids, the pH, the potential and the interfacial Gibbs energy, can be useful in the analysis of some primitive motile mechanisms of whole cells, of their organelles and the streaming phenomena of the cytoplasm. The electrocapillary motion generated by the Marangoni effect in the present model system, can give an explanation for the effects of direct electric current on the locomotion of amoebae [24]. It has been repeatedly observed that *Ameoba proteus* moves towards the negative electrode when a potential difference is applied to a solution containing this organism [25,26]. A simple rationalisation of these observations is the onset of a surface-tension-driven motion at the outer cell membrane caused by the difference in potential, and hence, in interfacial tension between the leading and trailing edges of the cell.

The driving force in this case, is identical to that causing the movement of the organic liquid droplet shown in Fig. 2 and the mechanism proposed gives a very simple interpretation for cell movements in applied fields.

Another interesting consequence of the potential- and pH-driven Marangoni motions at lipid membranes, can be the establishment of streaming patterns in the cytoplasm resulting from localised proton gradients. These can have self-sustaining characteristics if the driving force for the proton gradient is mass-transfer-controlled, i.e., if the reaction responsible for it is localised at a cell membrane, and its rate is determined by the mass transfer coefficients established by the cytoplasmic convective flow. Also, an elementary chemical recognition will be established by the proposed coupling, in which the cell membrane can sense and react to pH changes, local fields and nutrients that result in localised pH changes. The arguments presented are equally applicable to the movement of organelles in cells.

An interesting application of these ideas is in problems of phagocytosis and pinocytosis. Phagocytosis response is triggered by cationic particles [6], thus resulting in a localised change in surface charge in the region of attachment. The corresponding changes in local interfacial tension will depend on the lipid composition, and recent work [9] indicates that both increases and decreases in interfacial tension can be obtained for a given change in the state of charge. A local increase on attachment will result in rapid streaming of the plasma membrane towards the particle, tending to isolate it and pushing it inside the cell. The confirmation of these ideas on the nature of this elementary step requires further work which is currently in progress.

Cell motility is a complex phenomenon which has been the subject of much discussion and speculation [4,24,27,28]. For amoeboid movement, the contractile events are considered to be only part of the dynamic processes observed [3]. The charge effects of oriented phospholipid layers discussed above, can provide an elementary driving force for processes that are initiated at the cytoplasmic side of the membrane [3] and for the galvanotropic response of cells [29], in addition to the contractile mechanism based on the actin-myosin interactions [4].

Finally, it is important to give an estimate of the order of magnitude of the surface forces required to produce cytoplasmic streaming effects and to assess if these are of the right order of magnitude for surface-tension-driven processes. For this analysis, we shall use the data of Ewart [30] for the streaming in *Nitella* cells. The streaming cytoplasm was considered equivalent to the passage of liquid through a small tube. Although this is not quite the real situation, the hydrodynamic analogy is sufficiently accurate for the purpose of this discussion.

The quantity that must be compared is the shear stress generated at the cell wall by the flowing cytoplasm: if flow inside the cell is only due to the Marangoni effect, the shear stress ($\tau_w$) must equal the surface tension gradient, i.e.,

$$\tau_w = \frac{d\gamma}{dx} \tag{5}$$

Eqn. 5 results from the balance of forces at the boundary, since the shear induced by the flowing liquid must equal the shear resulting from the surface tension gradient. The average flow velocity measured by Ewart was of $3.3 \cdot 10^5$ m $\cdot$ s$^{-1}$; this corresponds to laminar flow conditions for the *Nitella* cell, and therefore, the shear stress at the wall is given by [28]:

$$\tau_w = \tfrac{1}{2} f \rho V^2 \tag{6}$$

where $f$ is the friction factor, $\rho$ the density and $V$ the average flow velocity. For laminar flow, the friction factor is given by [31]:

$$f = \frac{16}{R_e} \tag{7}$$

with the Reynolds number $R_e$ defined by:

$$R_e = \frac{du\rho}{\mu} \tag{8}$$

($d$ = characteristic dimension, diameter; $\mu$ = viscosity). Using the data of Ewart, a value of $\tau_w = 2.5 \cdot 10^{-3}$ N $\cdot$ m$^{-2}$ is calculated for the shear stress. This shear stress must be generated by a change of surface tension in 2 cm (the cell length) of $\Delta\gamma = \tau_w \times$ (cell length) $= 5 \cdot 10^{-2}$ mN $\cdot$ m$^{-1}$. Although this calculation is approximate, it shows

that the changes in interfacial tension required to generate streaming are of the right order of magnitude, i.e., they represent only a fraction of the total value of the interfacial tension of the cell membrane, which is of the order of 2 $mN \cdot m^{-1}$.

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