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Lateral electrophoresis versus 2D-diffusion

In a recent, stimulating article in *TIBS*[1], Kenneth R. Miller and Mary K. Lyon discuss the cause and function of thylakoid membrane stacking in chloroplasts and compare the heterogeneous membrane protein distribution observed in higher plants with a homogeneous distribution. In our view, a homogeneous distribution of membrane proteins in an energy-coupling membrane might be quite uncertain because of long-range forces which D. B. Kell[2] suspects to be the origin of the apparently too small diffusion coefficients of membrane proteins. These forces develop inevitably. Consider for example the CF_1-CF_0-ATP-synthase (= ATPase) of chloroplasts. During photophosphorylation, protons pumped into the thylakoids by the light-driven redox-chain flow back through the ATPase. This cyclic flow of protons not only generates a transmembrane difference of μ_{H^+} but also a local electrical and concentration gradient around the ATPase[3] which channels H^+ towards and away from the bulk phase to the catalytic site. In other words, the transmembrane $\Delta\,\mu_{H^+}$ at the site of ATP-synthesis and H^+-backflow is smaller than the $\Delta\,\mu_{H^+}$ generated by the light-driven redox H^+-pump because part of the generated $\Delta\,\mu_{H^+}$ is dissipated by the H^+-flow along the membranes, which at the outer side of the thylakoid results in a more positive electrical potential at the ATPase compared to neighbouring sites. This local electrical gradient is further increased by the lowered pH at this site, which leads to a higher degree of protonation of the prevalent negative surface charges[4]. The size of the gradient in electrochemical proton potential along the membrane surfaces depends *inter alia* on the proton mobility and the pH. The higher the pH, the larger will be that part of the redox chain-generated $\Delta\,\mu_{H^+}$ which is dissipated by the proton flow between ATPase and redox chain. Consequently, the steeper gradient in μ_{H^+} is expected at the thylakoid outside, where the pH is more alkaline (for a discussion of this point see Ref. 5 and references therein). However, a voltage gradient can exist even without a gradient in μ_{H^+}, if the voltage gradient is balanced by a corresponding pH gradient.

This local voltage gradient should lead to lateral electrophoresis[6] and, as the ATPase is itself negatively charged[4], to a mutual attraction of the ATPases, thereby amplifying the aforementioned effects and thus leading to a break of homogeneity. In accordance with this idea, the phosphorylated LHC (light harvesting complex) is found in the stroma thykaloids[7] where the ATPases are located.

Crucial to the suggested mechanism is the size of the lateral voltage gradient between two membrane sites that is required to effectively compartment a charged membrane protein species. If two points on the membrane located at the distance x are considered and the only 'forces' acting on the membrane proteins of a certain species are diffusion and electrophoresis, then the equilibrium distribution is described by equating the flows driven by the two 'forces':

$$c_{(x)} \cdot m \cdot \frac{\mathrm{d}v}{\mathrm{d}x} = D \cdot \frac{\mathrm{d}c}{\mathrm{d}x}$$

where $c_{(x)}$ is the local protein concentration $[n/l^2]$; m is the electrophoretic mobility $(l^2/(t \cdot V))$; D the diffusion coefficient $[l^2/t]$; $\mathrm{d}v/\mathrm{d}x$ and $\mathrm{d}c/\mathrm{d}x$ are the respective voltage concentration gradients and n, l, t, V are the number of particles, the units of length, time and electrical potential, respectively.

If $\mathrm{d}v/\mathrm{d}x$ is assumed to be constant $(= \Delta v/\Delta x)$ between the two points considered, the above equation yields an ordinary differential equation:

$$\frac{\mathrm{d}c}{\mathrm{d}x}(x) = \frac{m}{D} \cdot \frac{\Delta v}{\Delta x} \cdot c_{(x)}$$

with the solution

$$c_x = c_0 \cdot \exp\left(\frac{m}{D} \cdot \frac{\Delta v}{\Delta x} \cdot x\right)$$

$$= c_0 \cdot \exp\left(\frac{m}{D}\,\Delta v\right)$$

(c_x and c_0 are the concentrations at two points), i.e. the achieved accumulation c_0/c_x is in the first approximation independent of the length-scale (the time needed for reaching this equilibrium distribution is of course not independent of x, compare for example[6,8,9], but c_0/c_x is dependent on the voltage drop between the two points and on $D/m[V]$, which gives the voltage difference that is needed for a concentration ratio of $1/e$.

Jaffe[6] considered lateral electrophoresis along a membrane as a natural phenomenon and showed that the parameter D/m is independent of the drag encountered by the membrane proteins and estimates D/m of a spherical 10 nm-particle to be 1.3 mV. A voltage drop of this size seems inevitable near the proton and/or charge conducting proteins of the various energy coupling membranes; thus the heterogeneity cannot easily be avoided, because it develops as soon as the membrane is energized; experimental clues for thylakoid membrane particle rearrangement upon energization are given in Ref. 10. On the other hand, electrophoresis could serve to regulate and direct the flow of redox equivalents between the components of energy coupling membranes.

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