Active Membranes

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Abstract

The question is addressed as to how non-equilibrium conditions control the large-scale properties of membranes.

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Morphology and fluctuations of membranes around equilibrium have been extensively studied for several decades.

First, fluid membranes have been investigated, then multicomponents membranes, and sophisticated in-plane order, such as hexatic order, have been considered. Very interesting notions, such as the "crumpling" transition, and the entropic repulsive force, spontaneous curvature, gaussian curvature, etc, have emerged from these studies, and have been tested experimentally.

Whereas the concepts, developed for describing membranes close to equilibrium, are certainly useful for understanding some important properties of biological membranes, they do not retain a very important feature, namely the out-of-equilibrium activity taking place on, or in the vicinity of the membrane. This activity is, in general, very specific like in transport by pumps or channels, or surface polymerization of filaments like actin, proteins synthesis, exocytosis, endocytosis, etc. Considering this specificity, it might well be that no general law governing these membranes could be expected. This is, as a matter of fact, probably true for the short-scale behavior.

Under such circumstances, the first sensible attitude is to study individual problems, one at a time, as was done, for instance, with ion channels using patch clamp techniques. We know however, from our past experience in many other fields of research, that even when local processes are complex and specific, large-scale properties may obey simple generic rules. A natural question to raise is then: in what way does a membrane, in which local chemistry takes place, differ on large scales, from a membrane close to equilibrium? There are certainly many aspects to this question: one, very basic and practically unaddressed, concerns the sta-

tistical ensemble in which the membrane should be described. The constant number of molecules ensemble valid for the description of vesicles, is obviously inappropriate for real biological membranes. The constant tension ensemble, valid for black films in the presence of a plateau border, is probably closer to reality since there is a large surface reservoir in the endoplasmic reticulum.

However, exchanges in the cell are regulated "actively", and what is maintained constant is not clear. On a "semi-local" scale, the usual notions of tension, curvature modulus, etc., are probably still correct. The most salient difference with situations close to equilibrium, comes from the fact that the noise acting on the membrane now does not satisfy the fluctuation-dissipation theorem. "Chemical noise" has two components, one stemming from the transient nature of the chemical process (which we call shot noise), another one stemming from concentration fluctuations of the noise sources (e.g. protein concentration fluctuations).

We discuss several consequences resulting from the existence of this noise; in particular, we show how membranes can "recognize" the presence of a nearby wall and change its fluctuation amplitude accordingly (Prost et al., 1996; Prost et al., 1998). We also discuss the nature of a new instability, which arises when the noise sources redistribute in response to membrane curvature (Ramaswany et al., in preparation).

We eventually evaluate orders of magnitude corresponding to experimental situations (Manneville et al., in preparation), and discuss the biological relevance of these considerations.

References

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