LIPID MEMBRANE FLUCTUATIONS DRIVE ORDERED DOMAINS STACKING AND ALIGNMENT

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We show that membrane shape fluctuations can play the role of the driving force of membrane structures self-organization. We identify the mechanism of interbilayer and transbilayer coupling of liquid-ordered domains in lipid membranes. The driving force for such coupling has thus far remained unrevealed, yet number of experiments show that liquid-ordered domains demonstrate transbilayer correlative behaviour by uniting into stacks in the multilamellar structures and membrane domains are always adopt bilayer conformation. Various hypothesis were put forward to explain coupling phenomena. Transbilayer coupling is usually explained by some phenomenological interaction between ordered and disordered domains in opposite monolayers. While interbilayer coupling is described by hydration forces that are supposed to be different for ordered and disordered phases. Both hypotheses lack sufficient evidence and theoretical basis, while such a widespread cooperative behaviour of rafts makes to suggest the existence of common driving force for these phenomena. We provide the universal mechanism of such striking behaviour. Using continuum elasticity theory, we show that elastic deformations alone are the driving force of ordered domain coupling. The coupling is provided by membrane dynamic shape fluctuations; the corresponding energy is proportional to domain area. This mechanism utilizes the idea that stiff regions in both monolayers attract each other because their registration minimizes spatial restraints on membrane undulations, i.e. domain registration maximizes entropy. We also discuss the influence of the domain «ground state», i.e. the deformation configuration corresponding to the membrane minimal energy. We show that it leads to the the coupling energy proportional to domain boundary length. Combination of these two mechanisms results in alignment driven by lipid deformations, the membranes fundamental property, which does not require introducing any specific features, like interactions at the membrane midplane, different hydration forces, etc. Fluctuation-based model is universal and does not depend on particular properties of lipid membrane and can be applied to any system, composed of elastic films with non-uniform elastic characteristics.