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Solvent hydrodynamics enhances the collective diffusion of membrane lipids

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Our work unveils a new and generic mechanism for collective lipid diffusion in membranes which is due to the hydrodynamic interaction between the membrane and the embedding solvent. Since 1975, the collective dynamics of membrane lipids have been described by the celebrated Saffman-Delbrück (SD) theory which predicts the slowing down of large flow patterns of lipids due to the solvent's *tangential* friction on the membrane[1]. Following the SD theory, lipid flow patterns smaller than the Saffman length $\lambda_{\rm S}$ (about one micron) are thought to be unaffected by the solvent traction, leading to the believe that the lipid hydrodynamics at submicron scale is essentially 2D, with negligible momentum exchange with the solvent.

We show that this conclusion is incorrect and in this respect prove that the SD theory is incomplete. We performed molecular dynamics and coarse-grained models with implicit 3D hydrodynamics and find that the ambient liquid strongly enhances the collective diffusion of lipids at all scales, even much smaller than λ_s . Our findings match quantitatively with the theoretical predictions for the anomalous collective diffusion of colloids confined in a 2D plane but embedded in a 3D solvent [2, 3]. While SD theory considers the solvent tangent traction on the membrane, we find that the solvent momentum in normal direction spreads tangentially over the plane creating long-ranged repulsive hydrodynamic forces between lipids. The resulting collective diffusion becomes anomalous, increasing proportionally to the disturbance wavelength. This phenomena is dominant over at least 100 nanoseconds, gradually decaying at long times, leading to the expected Saffman-Debruck membrane hydrodynamics.

Our results at large wavenumbers are in good agreement with spin echo experiments [4] and confirm the existence of strong localized lipid currents [5], probably related to the described phenomena. The life-span of the present phenomena (submicron scales and hundred of nanoseconds and below) is a new milestone in the understanding of the collective mo-



Fig. 1. Averaged velocity field evaluated from lipid displacements with respect to a central tagged lipid. Colour box represent the modulus of the velocity field.

tion of lipids, key for many biological process such as the spontaneous nanopore formation, kinetics of lipid rafts and protein collective motion, to name a few.

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