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## Tilt-induced clustering of cell adhesion proteins

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Cell adhesion proteins are transmembrane proteins that play a crucial role in the binding of cells to one another, as well as to the extracellular matrix that surrounds them. Cell adhesion proteins can typically organize into clusters that can take various forms, from circular patches to long linear structures. Here, we propose that the tilt between the extracellular protein domain and the cell membrane could trigger a clustering mechanism. Based on a Flory-Huggins-type framework, we show that the coupling between the membrane undulation and the symmetry-breaking effect of the protein tilt yields an effective line tension that is negative, allowing for stable clusters to form. Our model predicts a variety of clustering patterns, including the experimentally observed circular patches and long linear structures, as well as curved lines, rings, Turing-like patterns, or cross-linked networks, depending on the strength of the membrane-protein tilt and the chemical potential of protein binding. Our findings suggest a potentially critical role of the tilt effect of cell adhesion proteins in regulating the cluster formation of cell adhesion proteins.

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