# Up & Down: membrane waves driven by curved activators of actin polymerization

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*Short Abstract* — **Dorsal ruffles are propagating membranal waves that are related to cell processes such as endocytosis. Experimentally, ruffles have been associated with the actin cytoskeleton and membrane bound activators. We present a model which may explain the formation of these waves due to the interplay between membrane-bound activators of actin polymerization of opposite curvature. We analyze this model using linear stability analysis and map the dynamical phase diagram as a function of the activation levels of the two curved proteins. We present several testable predictions which can validate our model.**

## I. Introduction

FOR several years dorsal ruffles have been observed experimentally [1]. These ruffles are circular membrane undulations which propagate towards their center, eventually forming a closed vesicle at the convergent center of the wave. These ruffles are involved in endocytic-like processes, the internalization of the cell membrane and its receptors. These dynamic structures are driven by actin polymerization [1,2]. A previous model to describe such waves [3], relied on contractile forces produced by myosin II motors, in conjunction with convex actin activators. Nevertheless, our experiments demonstrate that the inhibition of myosin does not significantly reduce the amount of cells which have ruffles.

There is evidence that actin activators are recruited to ruffles by a curved membrane protein called Tuba [4], which contains a BAR domain [5] and is known to bend membranes in a concave shape [6]. New experimental observations indicate the localization in ruffles of IRSp53 protein, which contains a MIM domain that induces convex membrane shape [7], and also recruits actin activating proteins [8]. Motivated by these observations we propose a model for dorsal ruffles, which is based on the interplay between membrane activators of actin that are both convex and concave in shape.

## II. Model Details

Our model is a mean-field, continuum model of the membrane with the concentration fields of the two activators. The dynamics are governed by a Helfrich Hamiltonian where the bending energy is proportional to the mismatch between the membrane curvature and the spontaneous curvature of the curved activators. Each type of activator was analyzed with a single type of dynamic, either membrane-bound diffusion or adsorption from the cell cytoplasm. For the adsorption dynamics, the rate constants of the binding/unbinding process are governed by a Boltzmann factor of the mismatch in the bending energy between the membrane's curvature and the activator's spontaneous curvature.

## III. Results

Using linear stability analysis, we map the conditions that allow the formation of unstable waves, as a function of the type of dynamics of the activators, and their levels of activity. In the case where the two activators have the same type of dynamics, wave instability occurs only when the convex activator is more mobile than the concave one. When the type of dynamics of the two activators is different, there is always a region of the phase diagram that contains unstable waves. Regions with Turing instability always appear, independent of the type of dynamics. We also analyzed the group velocity of these waves, comparing with experimental results [4].

## IV. Conclusion

The combination of convex and concave actin activators produces a wealth of behaviors. Future comparisons with experiments will allow us to validate this model with respect to observed ruffles.

### References

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