MAR17-2016-020029

Abstract for an Invited Paper
for the MAR17 Meeting of
the American Physical Society

**Collective gradient sensing: fundamental bounds, cluster mechanics, and cell-to-cell variability**[1]

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Many eukaryotic cells chemotax, sensing and following chemical gradients. However, experiments have shown that even under conditions when single cells do not chemotax, small clusters may still follow a gradient. Similar collective motion is also known to occur in response to gradients in substrate stiffness or electric potential (collective durotaxis or galvanotaxis). How can cell clusters sense a gradient that individual cells ignore? I discuss possible "collective guidance" mechanisms underlying this motion, where individual cells measure the mean value of the attractant, but need not measure its gradient to give rise to directional motility for a cell cluster. I show that the collective guidance hypothesis can be directly tested by looking for strong orientational effects in pairs of cells chemotaxing. Collective gradient sensing also has a new wrinkle in comparison to single-cell chemotaxis: to accurately determine a gradient direction, a cluster must integrate information from cells with highly variable properties. When is cell-to-cell variation a limiting factor in sensing accuracy? I provide some initial answers, and discuss how cell clusters can sense gradients in a way that is robust to cell-to-cell variation. Interestingly, these strategies may depend on the cluster's mechanics; I develop a bound that links the cluster's chemotactic accuracy and its rheology. This suggests that in some circumstances, mechanical transitions (e.g. unjamming) can control tactic accuracy.

[1]Work supported by NIH Grant No. P01 GM078586, NIH Grant No. F32GM110983