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Cells as strain-cued automata

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ABSTRACT

We argue in favor of representing living cells as automata and demonstrate that cells behaving as automata can form patterns by responding to local variations in the strain fields that arise due to their individual or collective motions. A cell's response to strain stimuli is assumed to be effected by internally generated, internally powered forces. The forces are a response to the stimulus of external strain conditions, but generally move the cell in directions other than those implied by external energy gradients, including any stresses associated with the stimulating strain fields. Estimates of the time rates of change of elastic strain energy and cell–cell adhesion energy in moving cell populations support the automata depiction: the strain and adhesion energies are orders of magnitude lower than the rate at which metabolic energy is generated by migrating cells. Thus migrating cells have abundant power available to choose to move regardless of, or even in opposition to, external energy gradients. We use new formulations of cells acting as automata to show that strain fields can provide pattern-forming instruction to cells. We use analysis of the case of ameloblasts moving during amelogenesis to demonstrate that, for a population of cells among which no chemical gradient or gradient in energy is known to exist, patterns can still arise as a result of kinetic feedback effects, providing individual cells act to enhance relative sliding motions in response to local shear strains. We also analyze the cases of angiogenesis and innervation of the gut to demonstrate that strain fields that arise when one type of cell invades a host population can guide the invading cells to form network structures if the invaders move to locations of high strain in the host, rather than to minimize strain energy. The strain cues act as the primitive symmetry-breaking signal that stabilizes the geometry of branches, as well as accounting for branch bifurcation and the formation of closed networks by branch coalescence. In each of the cases studied, the ratio of the rates of competing time dependent processes, migration velocity and a relaxation velocity, has a profound effect on morphological outcomes. We conjecture that nature uses rapid migration to achieve certain outcomes and slow migration to achieve others. We also infer, from analysis of network formation, a transition in the mechanical response of a cell from animate to inanimate behavior when the time rate of change of an applied strain exceeds 10^{-4}–10^{-3} s^{-1}, which is confirmed by recent in vitro experiments.