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# Mechanics of tissue compaction

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## Abstract

During embryonic development, tissues deform by a succession and combination of morphogenetic processes. Tissue compaction is the morphogenetic process by which a tissue adopts a tighter structure. Recent studies characterized the respective roles of cells' adhesive and contractile properties in tissue compaction. In this review, we formalize the mechanical and molecular principles of tissue compaction and we analyze through the prism of this framework several morphogenetic events: the compaction of the early mouse embryo, the formation of the fly retina, the segmentation of somites and the separation of germ layers during gastrulation.

During embryonic development or pathologies, the cohesion of cells within tissues can evolve significantly. Tissue compaction is a process by which cells increase their cohesion. During tissue compaction, cells get in closer contact with their neighbors, a process associated to the spreading of cells onto one another. Failure in compaction can result in severe pathologies, such as isolated left ventricular non-compaction cardiomyopathy [1], or developmental arrest, in particular during compaction of the mammalian embryo [2,3]. Since adhesion molecules are essential to tissue compaction [4,5], this morphogenetic process is generally described as an adhesion process that is driven by adhesive forces [6-9]. However, recent measurements challenge the idea that adhesion molecules would be able to generate sufficient forces to deform tissues [10,11]. As any tissue shape change, tissue compaction results from the combined action of intra- and inter-cellular forces, which are not solely of adhesive nature. We will describe in this review how compaction relies in fact on the adhesive and tensile properties at cells' surface, which are controlled by the adhesion and contractile machineries of the cell. Understanding the forces involved in cell-cell interactions is therefore essential to apprehend tissue compaction beyond its molecular aspect. In this review, we initially formalize the process of compaction and then use this framework to interpret several morphogenetic processes during embryonic development that involve some degree of tissue compaction.

## Mechanics of tissue compaction

Tissue compaction is a fundamental morphogenetic process that relies on cells mechanical interactions. This mechanical coupling between cells is primarily governed by their surface properties. The spreading of a cellular interface is hence controlled by two main properties: adhesion, which fosters interface spreading, and surface tension, which, on the contrary, promotes interface shrinkage. In fact, adhesion and tension, despite being of distinct

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