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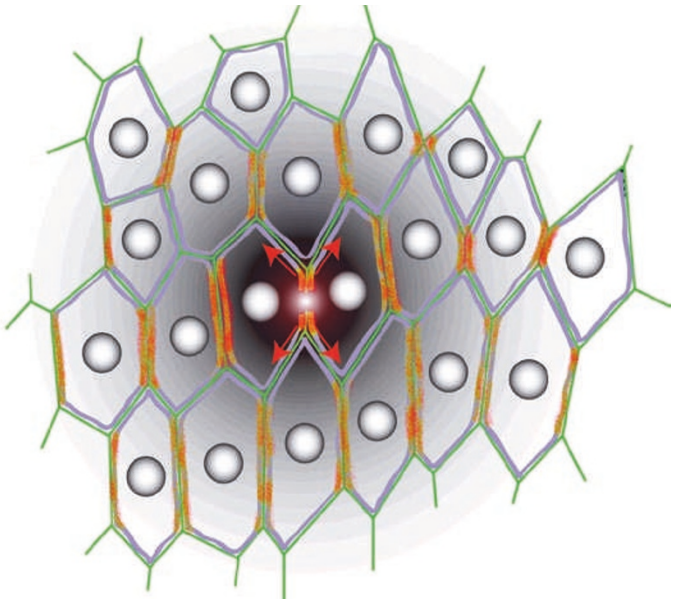
MECHANOTRANSDUCTION

Under tension

The early developmental stages from an egg to a detailed body plan differ between species, but are often characterized by common structural rearrangements. In addition to the indispensable functions of genetic programmes in regulating development, tissues are shaped by mechanical forces. But what are the origins and the nature of these forces? Can they drive cell shape changes and tissue dynamics? And how are they spatially distributed at the tissue scale? Two studies now address some of these questions during *Drosophila melanogaster* development.

> “…tissues are shaped by mechanical forces.”



A scheme that illustrates focal ablation in the centre of the image and relaxation of the actomyosin network (red arrows). Cell contacts are in green, actin in purple and myosin II polarized distribution in orange. Image courtesy of T. Lecuit and P. -F. Lenne, Université Aix-Marseille III & II, Marseille, France.

During *D. melanogaster* gastrulation, apical constriction of ventral cells facilitates the formation of a ventral furrow and the subsequent internalization of the presumptive mesoderm. Eric Wieschaus and colleagues investigated how myosin, which is known to localize to the apical cortex of constricting ventral furrow cells, produces force to drive constriction. Using real-time imaging and quantitative image analysis, they showed that the apical constriction of ventral furrow cells is pulsed — repeated constrictions, which were asynchronous between neighbouring cells, were interrupted by pauses in which the constricted state of the cell apex was maintained. Myosin spots on the apical cortex were dynamic, with apical myosin spots repeatedly increasing in intensity and moving together to form larger and more intense myosin structures at the medial apical cortex. These bursts of myosin accumulation were correlated with constriction pulses, which indicates that constriction is driven by contractions of the medial apical cortex.

The transcription factors Twist and Snail differentially regulate pulse constriction. In contrast to wild-type ventral cells, *twist* and *snail* mutants accumulated myosin predominantly at the cell junctions. Knockdown experiments indicated that expression of *snail* initiates actin–myosin network contractions, whereas expression of *twist* stabilizes the constricted state of the cell apex. The authors propose a ‘ratchet’ model for apical constriction in which phases of actin–myosin cytoskeleton contraction and stabilization are repeated to constrict the cell apex incrementally.

Mechanical forces shape many morphogenetic changes during *D. melanogaster* development, including the elongation of embryos. The underlying mechanism was the topic of a study by Thomas Lecuit, Pierre-François Lenne and colleagues, who followed individual cells in the whole tissue over time and measured cortical tension during germband elongation. During this process, polarized junction remodelling, which is controlled by the polarized enrichment of myosin II, drives cell neighbour exchange (intercalation). Using quantitative analysis and mathematical modelling, they showed that anisotropy of cortical tension at apical cell junctions is sufficient to drive junction shrinkage, cell intercalation and tissue elongation. Tension is anisotropically distributed and depends on myosin II accumulation. Further analysis of high-order structures showed that fluctuations in the apical cortex facilitated intercalation, which suggested the existence of additional forces to those acting at cell junctions.

These experimental approaches should be applicable in other developmental contexts. By estimating tension *in vivo*, it will be possible to test how external and internal forces cooperate to drive the variety of forms and patterns observed during tissue morphogenesis, and to determine whether such forces feed back on other developmental processes.

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ORIGINAL RESEARCH PAPERS Martin, A. C. *et al.* Pulsed contractions of an actin–myosin network drive apical constriction. *Nature* 23 Nov 2008 (doi:10.1038/nature07522) | Rauzi, M. *et al.* Nature and anisotropy of cortical forces orienting *Drosophila* tissue morphogenesis. *Nature Cell Biol.* 2 Nov 2008 (doi:10.1038/ncb1798)