



## INTRODUCTION

# Forceful Thinking

TRANSFORMING A SINGLE FERTILIZED EGG INTO A COMPLEX ANIMAL IS A MARVEL and a mystery. Decades of study have identified molecules and mechanisms for specific steps in this transformation. But far more is involved in the construction process than the simple conversion of undifferentiated cells to a defined fate. When gazing at the stages from embryo to adult, it is clear that a multitude of cell movements and deformations (compression, extension, intercalation, and rearrangement, to name a few) are at play to shape the folds, cavities, and appendages. How do these dynamic activities come about? Biomechanics is a likely contributor, with forces exerted by the environment as well as by contractile and protrusive activities between cells. Investigators with expertise in physics and computational biology collaborate with developmental biologists to understand how forces shape animal form. *Science's* special section titled Forces in Development highlights but a few such advances in the application of physical reasoning to developmental events.

Many tissue patterns result from the interpretation of a concentration gradient of diffusible chemical substances, called morphogens, by cellular signaling cascades and transcriptional networks. As outlined by Kicheva *et al.* (p. 210), biophysical models, genetics, and quantitative imaging have been applied in the embryo to elucidate morphogen behavior and pattern readout for the coordination of events across molecular, cellular, and tissue scales. Physical reasoning has also advanced our understanding of how cells of different fate are sorted or compartmentalized. Amack and Manning (p. 212) review surface tension as important for tissue boundaries, but describe more recent work showing that adhesive molecules and mechanical polarization are also key.

Besides measuring physical elements, alternative theoretical views assist in understanding development. Furusawa and Kaneko (p. 215) discuss a dynamical systems approach to the transition between stem cells and differentiated cells. This Perspective highlights the importance of cell-cell interactions and oscillations in transcription and protein expression and is instrumental in the application of quantitative analyses to explain stem cell behavior. Finally, Newman (p. 217) notes that stereotypical morphological motifs that generate tissues that elongate, fold, and segment show similarity to the outcomes of physical processes with condensed, chemically active, viscoelastic materials. It is suggested that physical processes came into play when mobilized by ancient genes in a multicellular context for the establishment of animal form.

Technological advances have enabled the studies above, but such interest is not new. Ray Keller (p. 201) reminds us of work from the mid-19th century, when embryologists explored developmental mechanics and the forces generated by cells shaping the embryo. Going forward, the combination of technological improvements with physical and biological approaches should yield ever more clarity to understanding the biomechanics underlying development.

— BEVERLY A. PURNELL

## Forces in Development

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The above series shows the dynamics that localize zebrafish sensory cells.

# Science

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