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Regulation of gastrulation movements by emergent cell and tissue interactions

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It is during gastrulation that the primordial germ layers are specified, embryonic axes become morphologically manifest, and the embryonic body plan begins to take shape. As morphogenetic movements push and pull nascent tissues into position within the gastrula, new interactions are established between neighboring cells and tissues. These interactions represent an emergent property within gastrulating embryos, and serve to regulate and promote ensuing morphogenesis that establishes the next set of cell/tissue contacts, and so on. Several recent studies demonstrate the critical roles of such interactions during gastrulation, including those between germ layers, along embryonic axes, and at tissue boundaries. Emergent tissue interactions result from – and result in – morphogen signaling, cell contacts, and mechanical forces within the gastrula. Together, these comprise a dynamic and complex regulatory cascade that drives gastrulation morphogenesis.

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Introduction

Lewis Wolpert is credited with saying that "*it is not birth, marriage, or death, but gastrulation that is the most important time of our lives*". Indeed, he has a point: a great many critical events comprise this relatively short phase of embryonic development. At its conception, the embryo consists only of a mound of pluripotent cells, but by gastrulation's end, an animal form has begun to take shape. It is during gastrulation that the anteroposterior (AP) and dorsoventral (DV) embryonic axes are established, the primordial germ layers are specified, internalized, and subsequently shaped into a rudimentary body plan with organ anlagen. Newly formed tissues thin and expand by epiboly movements, and lengthen along the nascent AP axis during gastrulation concomitant with mediolateral (ML) narrowing in a highly conserved process termed convergence and extension (C&E) [1]. This taking of shape, or morphogenesis, is the essence of gastrulation, and is accomplished through an intricate series of individual cell and collective tissue behaviors that are precisely coordinated in both space and time with embryonic axis formation (reviewed in Ref. [2]).

It has long been understood that signaling molecules, termed morphogens, diffuse throughout the developing embryo to instruct the fate of cells in a concentration-dependent manner. Localized sources of such morphogens and their antagonists establish gradients across an entire embryo or tissue, and thus affect the fate and behavior of cells at a distance [3,4]. Many embryos possess small regions termed 'organizers' that are the source of many morphogens simultaneously, and which function during gastrulation to orchestrate cell fates and morphogenetic behaviors throughout the entire embryo [5,6]. Such global signaling patterns AP and DV body axes, specifies germ layers, patterns tissue sub-types, and regulates gastrulation movements [7]. As this inductive cascade unfolds, new cellular interactions are established: between cells of adjacent germ layers, between neighbors with different positional values along an axis, and at tissue boundaries within the nascent germ layers (see graphical abstract). These cellular interactions in turn inform subsequent morphogenetic movements, and therefore comprise an emergent aspect of gastrulation. Each is regulated by a distinct set of molecules, and each produces a distinct cell behavior that contributes to proper shaping of the embryo. In this review, we discuss recent advances in our understanding of dynamic cellular interactions that drive morphogenesis during gastrulation and their underlying cellular and molecular mechanisms.

Interactions between cells of adjacent germ layers

At the onset of gastrulation, mesoderm and endoderm germ layers internalize through the blastopore (or its equivalent) and the mesoderm comes to lie between the deep endoderm and superficial ectoderm. New interactions are therefore established between cells within adjacent germ layers, and these vertical interactions are critical to gastrulation morphogenesis. Although cells of different germ layers can and do interact, they must also form stable boundaries between them that keep the layers segregated. In *Xenopus* embryos, separation of