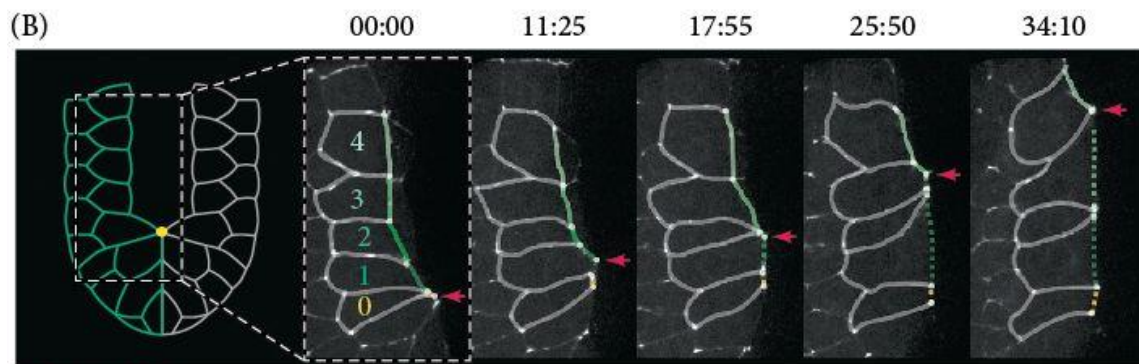
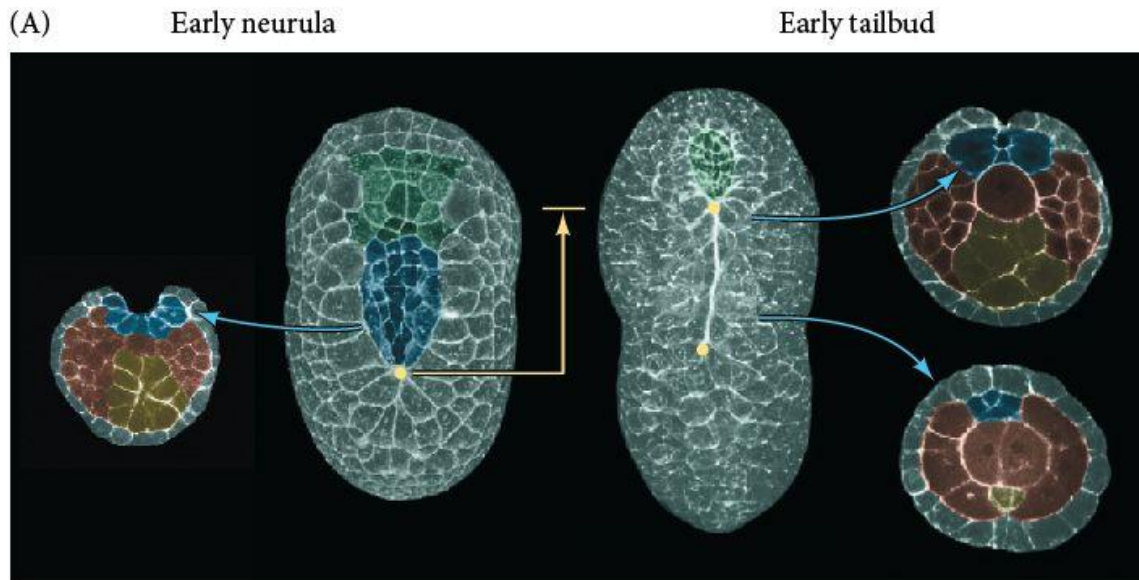
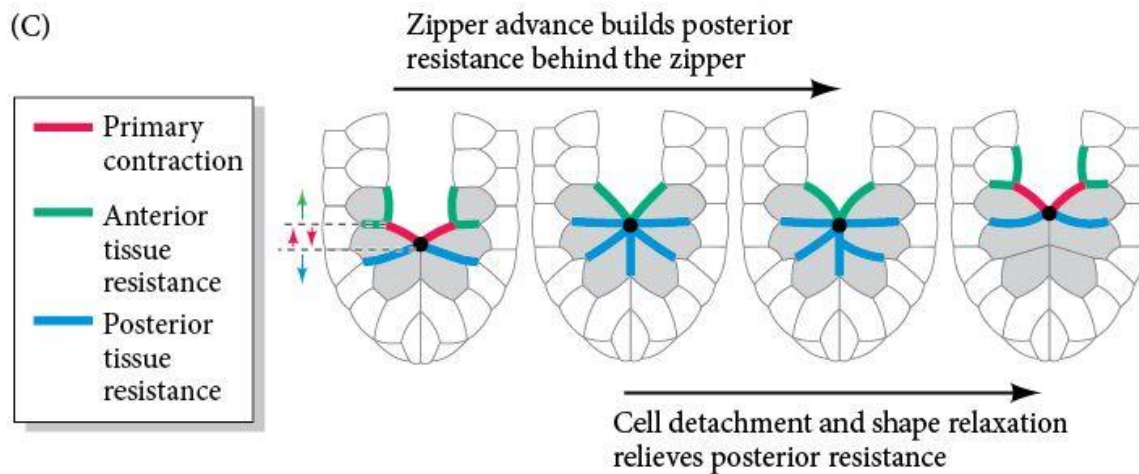


The Biomechanics of Neural Fold Zippering Revealed by the Ancestral Chordate

Visualizing neural tube zipping in the mouse revealed cell behaviors at the time of fusion, but what are the forces driving this attachment of the apposing neural folds? To better quantify the mechanisms of neural tube zipping, we will examine a simpler vertebrate system, that of *Ciona intestinalis*. Tunicates (also called ascidians) such as *Ciona* form a neural tube through primary neurulation, which includes a very similar zipper-like fusion event that proceeds in a posterior-to-anterior direction (Figure 1A; Nicol and Meinertzhagen 1988a,b; Hashimoto et al. 2015). Live-cell imaging of the membrane junction points between epidermal and neural cells during neural tube closure revealed a mechanism of sequential exchange of junctions at apical membrane junctions (Figure 1B). The driving force for zipper advancement in *Ciona* may be the localized activation of actomyosin contraction (i.e., myosin moving on filamentous actin) in the apical membranes of epidermal cells lying immediately ahead of the zipper point (Figure 1C). Junctional tension is highest between the apical membrane of these epidermal cells and their adjacent neural ectodermal neighbors. Moreover, inhibition of myosin prevents zipper advancement. These data suggest that a stepwise exchange of cell junctions is initiated by the apical activation of actomyosin contraction, which is then followed by a release in the attachments of posterior junctions to the zipper point and consequently a reduction in posterior resistance. As a result of these junctional exchanges, epidermal-to-neural attachments are replaced with epidermal-to-epidermal adhesion, and neural tube closure advances (Hashimoto et al. 2015).



ZO-1 :: GFP No GFP



After: H. Hashimoto et al. 2015. *Dev Cell* 32: 241-255.

Figure 1 Neural tube zipper advance in *Ciona*. (A) *Ciona* embryos stained with phalloidin to label cell membranes at the early neurula and early tailbud stages. Corresponding transverse sections showing the neural (blue) and non-neural (gray) ectoderm are shown to the sides of these embryos (teal arrows). Closure of the neural tube progresses in a posterior to anterior direction, which is represented by the yellow progression points and yellow arrow. (B) Time-lapse imaging of an embryo expressing GFP in the membranes of cells of the left hemisphere. The schematic on the left illustrates the region being imaged. Cell membranes are outlined in color to indicate important cell junctions. Epidermal-to-epidermal cell

junctions are white; epithelial-to-neural cell junctions are in color. Arrow positions denote the location of the advancing rostral closure point. The critical observation is the correlation between zipper point advancement and the exchange of an epithelial-to-neural junction (solid colored lines) with a newly formed epithelial-to-epithelial junction (dashed colored lines). (C) Model for zipper advancement. Myosin contraction (red) pulls the zipper point anteriorly to the next cell junction (green), an event that occurs when the posterior attachments are finally released.

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