

ORIGINAL ARTICLE

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Morphogenetic movements during axolotl neural tube formation tracked by digital imaging

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Abstract During neurulation in vertebrate embryos, epithelial cells of the neural plate undergo complex morphogenetic movements that culminate in rolling of the plate into a tube. Resolution of the determinants of this process requires an understanding of the precise movements of cells within the epithelial sheet. A computer algorithm that allows automated tracking of epithelial cells visible in digitized video images is presented. It is used to quantify the displacement field associated with morphogenetic movements in the axolotl (*Ambystoma mexicanum*) neural plate during normal neural tube formation. Movements from lateral to medial, axial elongations and area changes are calculated from the displacement field data and plotted as functions of time. Regional and temporal differences are identified. The approach presented is suitable for analyzing a wide variety of morphogenetic movements.

Key words Cell tracking · Morphogenetic movements · Image processing · Neurulation · Axolotl

Introduction

Morphogenetic movements in epithelial sheets are one of the distinctive features of early embryonic development.

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One such process that has received much attention is neurulation, and in amphibian embryos, as in most vertebrates, neural plate cells undergo complex morphogenetic movements that culminate in rolling of the neural plate into a tube. The forces that drive the seemingly simple shape changes that are necessary for successful neural tube closure have been a subject of intensive investigation for some time (Roux 1888; Jacobson 1962; Burnside and Jacobson 1968; Jacobson and Gordon 1976; Lee and Nagele 1988; Schoenwolf and Smith 1990). The morphology and mechanical role of cytoskeletal components as force-producing elements, have also been investigated (Burnside 1973; Nagele and Lee 1980; Gordon and Esner 1987; Brodland and Gordon 1990; Schoenwolf et al. 1988). The pattern of movements of cells and groups of cells during neural plate morphogenesis has also been a focus of study (Jacobson 1962; Burnside and Jacobson 1968; Keller 1978; Clausi and Brodland 1993).

Epithelial movements during neurulation have been tracked using a variety of techniques, all of which involve some form of time lapse imaging. In some experiments, particles have been strategically placed onto the embryo surface and carried along by morphogenetic movements (Spratt 1946). In other studies, vital dyes that color small groups of superficial and underlying cells (Jacobson 1962) have proved useful. Tracking based on rubber replicas that preserve cell surface shape has proved effective in plants (Green and Linstead 1990) and might be applicable to embryo studies. In embryos of species such as *Ambystoma mexicanum* and *Taricha torosa*, distinctive cell-cell pigment variations occur in the neural plate, allowing cell motions there to be tracked visually (Burnside and Jacobson 1968). This approach has the advantage of not requiring intrusion into or contact with the epithelium being studied.

Studies of morphogenetic movements have acquired renewed importance. This is due, in part, to recent advances in computer simulation techniques. Computer simulations of morphogenetic movements can now make use of known mechanical properties of cytoskeletal components and other structural components (Clausi and

