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Original Article

Evidence for non-axial A/P patterning in the nonneural ectoderm of *Xenopus* and zebrafish pregastrula embryos

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ABSTRACT Recent studies in early *Xenopus* and zebrafish embryos have demonstrated that posteriorizing, non-axial signals arising from outside the organizer (or shield) contribute to A/P patterning of the neural axis, in contradiction to the classical Spemann model in which such signals were proposed to be solely organizer derived. Our studies on the early expression of the transcription factors GATA-2 and 3 in both *Xenopus* and zebrafish nonneural ectoderm lend support to the existence of such non-axial signaling in the A/P axis. Thus we find that the earliest expression of GATA-2 and 3 is located in nonneural ectoderm and is strongly patterned in a graded manner along the A/P axis, being high anteriorly and absent from the most posterior regions. This results by early neurula stages in three broad zones: an anterior region which is positive for both GATA-2 and 3, a middle region which is positive for GATA-2 alone and a posterior region in which neither gene is expressed. These regions correspond to head, trunk and tail ectoderm and may represent the beginnings of functional segmentation of nonneural ectoderm, as suggested in the concept of the 'ectomere'. We find that A/P patterning of GATA expression in nonneural ectoderm may occur as early as late blastula/early gastrula stages. We investigate which posteriorizing signals might contribute to such distinct non axial ectodermal patterning in the A/P axis and provide evidence that both FGF and a Wnt family member contribute towards the final A/P pattern of GATA expression in nonneural ectoderm.

KEY WORDS: *A/P patterning, nonneural ectoderm, GATA factors, Xenopus, zebrafish, FGF, Wnt*

Introduction

The induction and patterning of the embryonic nervous system has been the focus of much experimental effort over a number of years [for reviews see (Doniach, 1992; Lumsden and Krumlauf, 1996)]. In contrast, very little is known about the formation and patterning of nonneural ectoderm. Recent experiments in early *Xenopus* and zebrafish embryos reveal the activity of posteriorizing, non-axial signals arising from outside the organizer (or shield) in contradiction to the classical Spemann model in which such signals were proposed to be solely organizer derived (Bang *et al.*, 1997; Woo and Fraser, 1997). Clearly such radial A/P signals should operate within nonneural as well as neural ectoderm, but, other than isolated reports of the expression in nonneural ectoderm of single hox genes (Condie and Harland, 1987; Kolm and Sive, 1995; von Bubnoff *et al.*, 1995), patterned gene expression within nonneural ectoderm has not been reported.

The importance of the nonneural ectoderm in early development is indicated by its role in a number of inductive epithelial-mesenchymal interactions which are required for early embryonic patterning. Thus ectodermal signaling to mesenchyme is important for initial patterning events in tooth development in urodeles (Lumsden, 1988), for the directional guidance of neural crest and migrating pronephric duct in axolotl (Lofberg *et al.*, 1985; Drawbridge *et al.*, 1995), and for the stimulation of hematopoietic differentiation within the blood islands in *Xenopus* (Maeno *et al.*, 1996). In early cranio-facial development, matrix mediated interactions between epithelia and mesenchyme, operating locally, are

Abbreviations used in this paper: A/P, antero/posterior; D/V, dorsal/ventral; nne, nonneural extoderm; bFGF, basic fibroblast growth factor; eFGF, embryonic fibroblast growth factor; RA, retinoic acid; BMP, bone morphogenic protein; MBT, mid blastula transition; TGF, transforming growth factor.

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