THE METAMERIC ORGANIZATION OF THE PRESOMITIC MESODERM AND SOMITE

SPECIFICATION IN THE MOUSE EMBRYO

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INTRODUCTION

The earliest expression of a metameric pattern in the mammalian embryo at the light microscopic level is the appearance of neuromeres in the neural tube (Neal, 1918; Adelman, 1925; Bartelmez, 1923) and the formation of somites in the paraxial mesoderm (Butcher, 1929; Rugh, 1968; Theiler, 1972). Somites, which are tandem blocks of mesodermal cells, are arranged in a craniocaudal series and they are formed by the successive segmentation of the paraxial mesoderm. Situated caudal to the most recently formed somite, there is a portion of the paraxial mesoderm which always remains overtly unsegmented. This tissue, which is known as the presomitic mesoderm in the mouse embryo, is contiguous with the tissue at the caudal end of the embryonic axis (Fig. 1). It is believed that an active recruitment of cells to the presomitic mesoderm occurs within the caudal region of the embryo through the activity of the primitive streak, and at a later stage, of the tail bud (Flint et al., 1978; Tam, 1981). The presomitic mesoderm in the mouse embryo is developmentally homologous to the caudal paraxial mesoderm of amphibian embryos (Woo Youn et al., 1980) and to the segmental plate of avian and reptilian embryos (Bellairs, 1979; Packard & Meier, 1983, 1984).

There is now mounting evidence that the cells in the segmental plate or the presomitic mesoderm are already determined for somite formation (Bellairs, 1985), but nonetheless, under experimental or unusual circumstances, some degree of regulation in the size and shape of somites can still occur during the differentiation of the presomitic mesoderm (Cooke, 1977; Menkes & Sandor, 1977). The ultimate appearance of a somite in the body axis seems to be the result of a gradual and orderly series of cellular events that proceed in a synchronized fashion through the presomitic mesoderm in a craniocaudal direction (Cooke, 1977; Pearson & Elsdale, 1979; Elsdale & Pearson, 1979; Cooke & Elsdale, 1980; Bellairs & Veini, 1984). Among these pre-programmed events are changes in cell shape, cell-to-cell adhesiveness, the extracellular matrix, the relations to surrounding epithelia, cellular motility and mitotic activity (Bellairs, 1979; Bellairs et al., 1978, 1980; Stern & Bellairs, 1984a; Lash et al., 1984; Cheney & Lash, 1984; Chernoff & Lash, 1981; Ostrovsky et al., 1983; Belousov & Naumidi, 1983; Lipton & Jacobson, 1974a; Flint & Ede, 1978). Since the segmentation of somites can still occur when the segmental plate is
Fig. 1. A scanning electron micrograph showing the paraxial mesoderm of an early-somite-stage mouse embryo. Three somites and one segmenting somite are found cranial to the presomitic mesoderm (PM) which extends to the primitive streak (PS). Bar = 100 μm.

Partially deprived of its normally associated epithelia (Bellairs, 1963; Bellairs & Veini, 1983; Packard & Jacobson, 1976) and that the craniocaudal sequence of segmentation is retained despite a reversal of the axial orientation of the segmental plate (Menkes & Sandor, 1977), it seems that the program of cellular differentiation has been stably imprinted upon the cells, the execution of which becomes autonomous and could be triggered by some chemical signals (see Lash, this volume).

Recent experimental and morphological evidence suggests very strongly that superimposed upon this orderly train of cellular events, there is an early meristic pattern in the presomitic mesoderm. Morphological observations made using stereoscopic techniques reveal a unique organization of the mesenchymal cells into circular domains of somitomeres. The somitomere was first discovered in the chick embryo by Meier (1979) who at that time was looking for evidence of segmentation in the cranial mesenchyme. A meristic pattern of somitomeres was subsequently found in both the cranial mesenchyme and the segmental plate of the chick embryo and this provided the first direct evidence for a complete and uninterrupted segmental pattern in the paraxial mesoderm of a vertebrate embryo (Meier, 1979, 1981, 1984). Since then, the presence of somitomeres has been described in the head region of a fish, the Medaka (Meier & Martindale, unpublished), the newt (Jacobson & Meier, 1984), the snapping turtle (Meier & Packard, 1984), the quail (Meier, 1982) and the mouse (Meier & Tam, 1982), and in the presomitic mesoderm or segmental plate of the snapping turtle (Packard & Meier, 1984), birds (Packard & Meier, 1983) and the mouse (Tam et al., 1982). It has been known for some time that when the segmental plates (which still possess the surrounding ectoderm and endoderm) of the snapping turtle and the avian embryos are explanted and cultured, a relatively constant number of somites is always generated (Packard, 1980a,b; Packard & Jacobson, 1976). The remarkable correlation between the number of potential somites contained in the segmental plate and that of somitomeres which could be recognized, and the demonstration of a one-to-one developmental relationship between the somitomere and the somite are compelling