



## Developmental Biology

Volume 131, Issue 1, January 1989, Pages 85-101

## Development of the enteric nervous system in the moth: II. Stereotyped cell migration precedes the differentiation of embryonic neurons

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The enteric plexus is a discrete portion of the enteric nervous system (ENS) in the larval moth *Manduca sexta*. It consists of a stereotyped array of nerves extending across specific regions of both the foregut and midgut. Within these nerves are approximately 400 neurons (the EP cells), which do not appear to be uniquely identifiable but exhibit a spectrum of morphological and biochemical phenotypes. In this report we have described the morphogenetic events by which the enteric plexus is created during embryogenesis and have characterized the morphological differentiation of the EP neurons. In particular, we have demonstrated a prominent role for stereotyped cellular migration in the formation of this region of the ENS. The neurons of the enteric plexus arise from the dorsal epithelium of the foregut in the form of a dense, triangular packet. Between 40 and 65% of embryogenesis, the cells of this packet become progressively dispersed by a sequence of migratory events: an initial, slow phase of migration that is circumferentially directed around the foregut, and a rapid, dispersing phase by which the EP cells achieve their mature distributions across the foregut and midgut surface. These migratory phases occur along defined pathways on the gut and result in cellular translocations of up to 250  $\mu\text{m}$ . In the early phase, some migrating neurons extend long axons in stereotyped directions, while others retain a simple bipolar morphology. Neurons of both morphological types are interspersed throughout the initial packet of cells and participate equally in the migratory process. Toward the end of migration, cells with the simpler morphology also extend axons along predictable pathways. Several additional subtypes subsequently differentiate in various regions within the plexus. The expression of specific peptidergic substances (related to the molluscan peptide Phe-Met-Arg-Phe-NH<sub>2</sub>, as described in the accompanying paper (P. F. Copenhagen and P. H. Taghert, 1988, *Dev. Biol.* **130**, 70–84) commences within the EP cell population only after these migratory phases are complete and can be correlated with the outcome of cellular migration: only neurons that navigate onto the midgut regions of the plexus subsequently exhibit the peptidergic phenotype. This system should provide an excellent model with which to examine the mechanisms underlying the migratory process and the potential roles of cellular migration in regulating neuronal differentiation.

CNS, central nervous system; DAB, 3,3'-diaminobenzidine tetrahydrochloride; ENS, enteric nervous system; EP, enteric plexus; FMRFamide, I, -phenylalanyl-I, -methionyl-I, -arginyl-I-phenylalaninamide; ga, garland cell; HRP, horseradish peroxidase; PBS, phosphate-buffered saline; RN, recurrent nerve; T, trachea

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