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NISHIKAWA K. (School of Biological Sciences, University of Kentucky, U.S.A.):
The development of spinal motor neurons in salamanders.

In lower vertebrates, there has been much confusion concerning the number of different morphological and functional types of motor neurons that appear in the spinal cord during development. Part of this confusion stems from the fact that motor neurons have been classified differently in embryos and adults, and these classifications have been confounded by some authors. The first motor neurons to appear during development are primary motor neurons. These are large, multipolar neurons, whose cell bodies are located dorsally within the ventrolateral gray matter. Secondary motor neurons appear later than primary motor neurons. These are small, unipolar, pear-shaped cells, whose cell bodies are located ventromedially, in the periventricular region. In adults, medial pear-shaped and lateral spindle-shaped motor neurons have been described. While it is clear that only the embryonic secondary motor neurons give rise to both medial and lateral motor neurons of adults, neither the processes of differentiation and migration, nor the functional significance of the medial and lateral motor neurons is well understood. In amniotes, the lateral motor neurons appear to innervate limb musculature and the medial motor column appears to innervate axial musculature. However, it is clear that the function of these motor neurons is different in anamniotes.

Our studies of the development of cervical spinal neurons have shown that salamanders exhibit three different types of motor neurons development, which are correlated with both phylogeny and type of embryonic development (larval vs. direct-developing species). In species with a free-living aquatic larval stage, such as *Salamandra salamandra* and *Eurycea bislineata*, only large primary motor neurons and medial pear-shaped secondary motor neurons are present at hatching. Later in development, some of these pear-shaped cells migrate laterally and differentiate into a splindle-shape form, passing through intermediate position before forming a highly organized column at the lateral margin of the gray matter. In the cervical spinal cord, lateral cone-shaped neurons also arise from medial pear-shaped neurons that migrate laterally. Some of these cone-shaped and spindle-shaped cells migrate outside the gray matter, into the lateral neuropil of the spinal cord near the ventral surface of the pia. Both types of laterally migrating neurons differentiate as they migrate. Differentiated cone-shaped and spindle-shaped neurons are never found in the periventricular region, but always farther laterally. In some direct-developing salamanders, such as *Desmognathus aeneus* and *Plethodon jordani*, the larval period occurs within the egg, and individuals are fully metamorphosed at hatching. In these species, lateral spindle-shaped and cone-shaped motor neurons are already present and fully differentiated at hatching.

Thus, in these direct-developing salamanders, it appears that cell migration and differentiation occur earlier in development relative to hatching than in salamanders with a free-living larval stage. In contrast, in one group of direct-developing salamanders, the bolitoglossine plethodontids, a very different developmental pattern is found. In a few individuals of these species, one or two spindle-shaped cells are found within the gray matter at the time of hatching. However, in most hatchlings, no spindle-shaped cells are present. Adults of these species are unique among vertebrates in that they entirely lack lateral spindle-shaped cells. These species are paedomorphic in that the pear-shaped cells neither migrate laterally nor do they differentiate into spindle-shaped or cone-shaped cells. While the functional significance of this failure to migrate and differentiate is unknown, we suggest that the developmental mechanism for paedomorphosis of the motor neurons in the spinal cord of these salamanders may be related to the extremely large genomes, which have been implicated in slowed developmental rates in other studies.