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THE DEVELOPMENT OF THE SYMPATHETIC NERVOUS SYSTEM IN BIRDS.*

BY ALBERT KUNTZ.

The present investigation of the development of the sympathetic nervous system in birds was undertaken in order to extend the writer's observations on the histogenesis of the sympathetic nervous system in mammals, and to point out certain morphogenetic differences in the development of the sympathetic system in birds and mammals, with a view to their phylogenetic significance.

In a recent paper** the writer has reviewed the literature bearing on the development of the sympathetic nervous system. Therefore, only such references to the literature will be made in this paper as seem to be necessary.

His, Jr. ('97)*** called attention to the fact that in the chick two pairs of sympathetic trunks arise in the course of ontogeny. These he characterized as the "primary" and the "secondary" sympathetic trunks. According to his observations, the cells giving rise to both the primary and the secondary sympathetic trunks are derived exclusively from the spinal ganglia.

My observations on the morphogenesis of the sympathetic trunks in the chick do not differ essentially from those of His, Jr. I find, however, that the cells giving rise to the primary and the secondary sympathetic trunks in the chick, like those giving rise to the sympathetic trunks in mammals, are derived, wholly or in part from the neural tube. From the third to the sixth day of incubation, medullary cells may be observed migrating into the ventral nerve-roots in considerable numbers. With similar cells which wander out from the spinal ganglia, these cells migrate peripherally along the spinal nerves. At a point a little above the level of the aorta, some of these cells deviate from the course of the spinal nerves and wander toward the dorso-lateral surfaces of the aorta where they become aggregated and give rise to the primary sympathetic trunks.

*From the Laboratories of Animal Biology of the State University of Iowa.

**The Development of the Sympathetic Nervous System in Mammals. Jour. Comp. Neurol. and Psychol., Vol. 20, No. 3, pp. 211-258.

***Ueber die Entwicklung des Bauchsympathicus beim Huhnchen und Menschen. Archiv. f. Anat. u. Entw., Supplement, 1897.

About the beginning of the sixth day, the anlagen of the secondary or permanent sympathetic trunks arise in the cervical and in the thoracic region, as ganglionic enlargements on the median sides of the spinal nerves just proximal to the origin of the communicating rami. These ganglionic enlargements are at first independent of each other, but become connected later by longitudinal commissures. There is as yet no evidence of the anlagen of the secondary sympathetic trunks posterior to the thoracic region.

As the secondary sympathetic trunks increase in size and importance, the primary sympathetic trunks decrease. At the close of the sixth day the anlagen of the secondary sympathetic trunks appear throughout the entire length of the body. The primary sympathetic trunks have become less conspicuous and in the thoracic region have completely disappeared.

The prevertebral plexuses are derived directly from the primary sympathetic trunks. About the middle of the fourth day, from the suprarenal bodies posteriorly, cells become separated from the primary sympathetic trunks and, migrating ventrally, become aggregated along the ventro-lateral aspects of the aorta and give rise to the prevertebral plexuses. These cell-aggregates show their greatest development in the sacral region. This condition in birds is obviously correlated with the enormous development of the ganglion of Remak. This ganglion arises toward the close of the fourth day, as an oval cell-column lying in the mesentery just dorsal to the rectum. Its greatest development occurs in the posterior region. It increases in size very rapidly until at the close of the fifth day it has become a large and conspicuous column of closely aggregated cells, with a maximum diameter of about 85 micra. Its diameter decreases anteriorly until it ends in the region of the genital ridges in a slender cellular cord which Remak has called the intestinal nerve (*Darmnerv*).

The ganglion of Remak was described by Onodi and by His, Jr., but as far as I have been able to learn, the cells composing it have never been traced to their source. My preparations show conclusively that the cells giving rise to this ganglion are derived directly from the anlagen of the hypogastric plexus.

His, Jr. has expressed the opinion that the elements composing the primary sympathetic trunks are resolved into the ganglia and the nerves of the peripheral sympathetic plexuses. In view of the comparatively enormous development of the prevertebral plexuses and the ganglion of Remak, this is obviously the fate of the primary sympathetic trunks in the posterior region of the body. There is no evidence, however, of

peripheral migration of cells from the primary sympathetic trunks in the anterior region. While there may be some migration posteriorly along the primary trunks, it is more probable that most of the cells in the anterior region are withdrawn into the secondary sympathetic trunks.

The vagal sympathetic plexuses; viz., the cardiac plexus and the sympathetic plexuses in the walls of the visceral organs, arise from cells which migrate from the vagus ganglia and the walls of the hind-brain along the fibers of the vagi. While medullary cells are migrating from the neural tube into the ventral roots of the spinal nerves, cells may also be traced from the walls of the hind-brain into the rootlets of the vagus and of the spinal accessory nerves. With similar cells which wander out from the vagus ganglia, these cells migrate peripherally along the vagi. In the thoracic region cells may be traced from the vagus trunks into the walls of the oesophagus where they become aggregated into cell-groups which constitute the anlagen of the myenteric and the submucous plexuses. These observations do not differ materially from the writer's observations on mammalian embryos. In mammalian embryos cells may be traced posteriorly from the anlagen of the myenteric and the submucous plexuses in the walls of the oesophagus and the stomach. These cells obviously give rise to the sympathetic plexuses in the walls of the intestine. In the chick, sympathetic cells cannot be traced posteriorly in the walls of the digestive tube with the same degree of definiteness. It is probable, however, that the cells giving rise to the sympathetic plexuses in the walls of the intestine are derived largely from this source. On the other hand, it is probable in view of the enormous development of the ganglion of Remak, that in birds many of the cells taking part in the development of the sympathetic plexuses in the posterior region of the intestine are derived directly from this ganglion.

At the bifurcation of the trachea, the vagus trunks bend laterally and ventrally round the bronchi until they come to lie close together along the ventral aspect of the oesophagus. A slender branch of each vagus trunk continues posteriorly from the bifurcation of the trachea along the lateral wall of the oesophagus. In transverse sections through the lungs, fibers accompanied by numerous cells may be seen to bend from these branches into the tissues of the lungs. These cells obviously give rise to the pulmonary plexuses.

About the close of the fifth day, in transverse sections through the heart, cells may be traced ventrally from the vagi toward the dorsal surface of the heart. In later stages these cells become aggregated into distinct groups in the septum of the atria and give rise to the cardiac plexus.

The above observations have shown that in birds, as in mammals, cells migrate peripherally from the neural tube and the cerebro-spinal ganglia, and that some of these cells give rise to the sympathetic nervous system. The cells giving rise to the sympathetic trunks and the prevertebral plexuses, including the ganglion of Remak, migrate peripherally along the spinal nerves, while the cells giving rise to the vagal sympathetic plexuses migrate peripherally along the vagi. The great majority of these migrant cells are the "indifferent" cells of Schaper, while a few cells occasionally are found among them which answer to the description of the "neuroblasts" of Schaper. This I have also shown to be the case in mammals. Mitotic figures occur occasionally along the paths of migration and in the sympathetic anlagen. We are not to suppose, therefore, that all the cells taking part in the development of the sympathetic system actually migrate as such from their sources in the neural tube and the cerebro-spinal ganglia. Doubtless, a goodly number arise by the mitotic division of "indifferent" cells along the course of migration. Inasmuch as these migrant cells are the "indifferent" cells and the "neuroblasts" of Schaper, they are homologous with the cells giving rise to the neurones and the neuroglia cells in the central nervous system. Therefore, the sympathetic system bears a direct genetic relationship to the central nervous system, and the sympathetic neurones are homologues with the efferent and the afferent components of the other functional divisions of the peripheral nervous system.