MORPHOLOGICAL CHARACTERISTICS OF CHEMOSENSORY,
VISUAL, AND STATOCYST PATHWAYS IN THE SNAIL

Helix lucorum

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The following structural characteristics of the chemosensory, visual, and vestibular pathways of the snail (Helix lucorum) were demonstrated by using a variety of histological techniques. Large and small neurons of the tentacle ganglion, the bipolar cells of the olfactory nerve, and a proportion of optic tentacle bulb chemoreceptors within the olfactory nerve all send their processes to the CNS of the mollusk. Here they are divided up into numerous bundles of fibers in the neuropil of the ipsilateral cerebral ganglion. They are joined by processes from the central nervous system put out by all neurons of the protocerebrum and the cluster of cells of the commissural section of the metacerebrum. Ocular receptors do not send processes down below the enlargement of the upper optic nerve. This enlargement is also the site where processes from cells within the CNS and the nerve itself terminate. An area of arborization of processes from the visual pathway cells is located in the neuropil of the pleural portion of the metacerebrum. Hair cells of statocysts put out processes to the cerebral ganglion, whence axons of small metacerebral neurons extend towards the organ of balance. Some processes from vestibular pathway cells form an arborization zone at the ipsilateral cerebral ganglion, while others pass through the cerebral commissure to form their area of arborization in the contralateral ganglion. Processes from vestibular and visual pathway cells arborize in exactly the same area.

INTRODUCTION

A wide range of techniques have been adopted by numerous authors for examining typical structural features of the chemosensory, visual, and vestibular pathways of Helix lucorum and other pulmonate mollusks [1, 2, 4, 7, 9, 11, 17, 18]. Even when taking all such findings together, no complete picture of how these three sensory pathways interrelate can be obtained, however. A few studies, now regarded as classical [9], employed methods inapplicable to all three structures. Other investigations, which used the most modern techniques [6-8, 11, 15, 17, 18], only produced a description of the peripheral regions of the sensory pathways. Yet other sets of findings contradict each other [2, 3, 13, 17]. Data obtained using electron microscopy, for example [17], indicate that hair cells (statosyst receptors of pulmonate mollusks) extend their processes to the vestibular nerve linking the balance organ with the CNS. No labeled receptor bodies were identified when cobalt chloride was used, during a study performed on the Helix lucorum, to stain the vestibular nerve travelling in the direction of the statocyst [4]. Laverak [13], moreover, observed that it is not hair cells but tiny microvillar cells, considered fundamental by almost all writers, which put out processes to the vestibular nerve in Helix lucorum.

All these contradictions, together with the fragmentary nature and inaccuracy of attempts to describe the sensory pathways of pulmonate mollusks point to the need for continuing with a full examination of how these pathways are structured using the latest techniques; interest in the subject has recently increased following findings [5, 10, 16] showing that plastic changes in the mollusk learning process take place at the level of the sensory neurons. Histological and histochemical techniques were therefore adopted to further our aim of studying the structure of the three sensory pathways in Helix lucorum.

METHOD

Investigations were performed on CNS preparations from over 150 Helix lucorum using two histological techniques and staining with the cobalt-lysine complex in three different modi-
Fig. 1. Structure of the peripheral areas of chemosensory and visual pathways. Diagram illustrates location of neurons in the optic tentacle bulb, the tentacle ganglion with finger-like projections, the upper segment of the olfactory nerve; also in the eye, the enlargement of the optic nerve, and the optical nerve itself, below the area of the enlargement; a-d) sites corresponding to photomicrographs in Fig. 4a-d. Arbitrary representation of numbers and dimensions of neurons.

fications. None of these methods provided a complete picture of a sensory pathway when used separately, but when combined could reveal the structure of all three pathways from receptor level to the cerebral ganglia cells. The fibers and somata of neurons sending processes to join the vestibular, optic, and olfactory nerves in both a centripetal and peripheral direction (towards the receptor), were stained using the technique of passive transport of the cobalt-lysine complex [12] (method 1). This technique involved placing the peripharyngeal nerve circle (if staining was to be directed towards the CNS) or the peripheral section of the nervous system (should it be directed towards the receptors) in a bath containing Ringer solution for cold-blooded animals. The severed nerve ending to be stained was transferred to a compartment filled with a solution of the cobalt-lysine complex, where it was left for three days and maintained at a temperature of 4-5°C. After precipitation of cobalt ions using sodium sulfide, the peripharyngeal circle was washed in Ringer's solution, fixed in Carnoy's solution, dehydrated in alcohol, and coated with balsam. Whole mollusk CNS preparations stained in this way were suitable for photography, but the finer points of the structures under study often remained unclear, particularly when the stained fibers were fine. An original modification of Pearson and O'Neill's [2] technique (method 1A) was used to intensify the contrast in lightly stained structures in the whole preparations; staining was heightened by silver salts. By this technique the finer points of the structure of the three sensory systems could be revealed, bypassing the stage of reconstruction by producing serial slices normally required by this method. The technique involved fixing the preparation, which had been stained using method 1, in Carnoy's solution, passing it through alcohol into water, and placing it in a 10-m1 vessel containing a solution of 40% NH₄NO₃ and 4%