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Golgi Impregnation and Retrograde Axonal Transport Studies of the Hypothalamo-Hypophysial System in the Arctic Lamprey, *Lampetra japonica*

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Abstract By using the Golgi impregnation methcd in the study of lamprey hypothalamus, it is demonstrated that the nucleus preopticus consists mainly of neurosecretory neurons similar to the type of CSF-contacting neurons. A small number of horizontal cells are also detected in this area. In addition to these cells another type of CSF-contacting neurons are seen in the ventral part of the nucleus preopticus. While both nucleus hypothalami dorsalis and nucleus hypothalami ventralis situated in the posterior part of the hypothalamus are occupied exclusively by the CSF-contacting neurons bearing the ventricular process, the nucleus recessus posterioris hypothalami in this area are found to have the neurons equipped with processes bearing varicosities that are projected toward the ventricular surface. Ten to 12 hours after the administration of HRP that is retrogradly transported in axon from the hypophysis, this agent appeared in several sites, such as the CSF-contacting neurons of the nucleus hypothalami ventralis and nucleus hypothalami dorsalis, both just above the pars nervosa, as well as neurosecretory neurons of the nucleus preopticus. These results may intimate that the pars nervosa of the lamprey hypophysis is innervated from the monoaminergic CSF-contacting neurons located in the lateral wall of the third ventricle, in addition to the neurosecretory nerve fibers.

Although the third ventricular wall of the hypothalamus of the lamprey is considered to be a relict descendant of the most primitive vertebrates, the presence of the cells equivallent to the cerebrospinal fluid (CSF)-cantacting neurons has been demonstrated in several ways, such as the fluorescence histochemistry of monoamine devised by Falck-Hillarp (Honma and Honma, 1970; Baumgarten, 1972; Konstantinova, 1973; Ochi and Hosoya, 1974), scanning electron microscopy by Shioda, et al. (1977), and transmission electron microscopy by Nakai et al. (1979). Vigh and his coworkers, through investigating of the CSF-contacting neurons of many kinds of vertebrates, have suggested that these cells are the possible elements concerning the neuro-endocrine correlation (Vigh and Vigh-Teichmann, 1973; Vigh-Teichmann and Vigh, 1974). In spite of these findings, studies on the detail of the CSF-contacting neuron in relation to its function have not yet been performed.

The distribution of monoaminergic fibers in the pars nervosa of the lamprey has already been reported (Baumgarten, 1972; Polenov et al., 1974; Tsuneki, 1974; Tsuneki and Gorbman, 1975; Tsuneki et el., 1975). However, the function and origin of these nerve fibers are still not clear. As Gorbman (1965) stated, there is no real median eminence in the hypothalamo-hypophysial system in the lamprey, which also lacks the portal vessel system flowing from the hypothalamus to the adenohypophysis. This evidence suggests that the hypothalamic control of the activity of glandular cell of the lamprey hypophysis is reasonably weak (Honma, 1969), and there might be some other way of hypothalamic control of the adenohypophysis.

Concerning this unanswered problem, the present study was planned to elucidate the basic architecture of the cellular components in the hypothalamus with emphasis on the morphology of the CSF-contacting neuron. Moreover, the shape and distribution of the cells which innervate and control the pars nervosa were also examined.

Material and methods

Adults of the arctic lamprey, *Lampetra*

japonica, were caught while migrating upstream for spawning, in the lower reaches of the Agano River and the Shinano River, situated in Niigata Prefecture facing the Japan Sea. The periods of collection were from January to March, 1976, and March to June, 1977.

1) Golgi impregnation: Twenty lampreys of both sexes were used in this examination. After decapitation, blocks of the brain with the area of third ventricle were processed following the rapid Golgi method. Selected cells of well impregnated sections were examined with a light microscope, some of them were traced and drawn with the use of a camera lucida.

2) Retrograde axonal transport of horseradish peroxidase (HRP): Eighteen lampreys of both sexes were kept in an aquarium in the laboratory for one to several days. First, the lampreys were anesthetized with 0.5‰ solution of MS 222 while cooling the body with ice. Then, the head was incised along the ventro-median line to disclose the hypophysis which is covered with the thick connective tissues (Larsen, 1965). After incision was made in the connective tissue sheath with a surgical knife, a little piece of the glandular tissue of pars intermedia or proximal pars distalis was removed with a forceps. The powder of 0.1 to 0.3 mg of horseradish peroxidase (Sigma type II) or 0.1 μl of HRP dissolved in 10% physiological saline was administered through the incision. After suturing the wound, the lamprey was kept alive in a tub of running water at 15°C for 3 to 12 hours.

The treated animal was then decapitated, and a block of the brain with hypophysis was removed. The block was immersed in the fixative consisting of 1% parformaldehyde and 1.25% gultaraldehyde solution in 0.1 M phosphate buffer, pH 7.2, at 4°C for 6 to 18 hours (La Vail, 1975). Following this, the block was rinsed in a solution of 0.1 M phosphate buffer (pH 7.3) containing 0.5% sucrose at 4°C for 12 hours. Then, the frozen block was cut on a cryostat to a thickness of 30 to 50 μm, collected in the buffer solution, and incubated in the solution consisting of 0.05% 3.3′-diaminobenzidine (Sigma) and 0.06% H_2O_2 for 3 to 10 minutes. After rinsing in buffer, the sections were mounted on a glass slide, and observed under a light microscope.

3) Histochemical demonstration of acetylcholinesterase: Five lampreys of both sexes were used for the demonstration of distribution in the activity of acetylcholinesterase by following Karnovsky and Roots' method (1964).

Results

The nucleus preopticus. The nucleus preopticus (NPO) consists of neurosecretory neurons with comparatively large perikarya and other kinds of cells. The neurosecretory neurons are located in deeper zones than in the cell group near the wall of the recessus preopticus of the third ventricle, just beneath the ependymal lining. Since almost all cells of the NPO are equipped with ventricular processes, the cells likely correspond to the CSF-contacting neurons (Fig. 1a, b, c, e, f). Among these cells, the pseudomonopolar type cells whose perikarya are spherical or ovoid in shape are also seen (Fig. 1b, e, f). Moreover, the cells without ventricular processes are also recognized, although their perikarya are located near the ventricle (Fig. 1d).

A slender axon from the outside of the perikaryon, either spherical or ovoid, projects and descends from the lateral side near the surface of the brain, and is pursued within the scope from 150 to 250 μm in length (Fig. 1a, b, d). In general, the process of neurosecretory neuron is rather thick, the spine of which is hardly seen, and no typical dendrite is discernible. A fine branch projecting perpendicularly from midway in the ventricular process is occasionally detected. The tip of the ventricular process forms a bulbous structure and terminates on the ventricular surface.

A special type of CSF-contacting neuron was seldom seen in the ventral part of the NPO, just above the optic chiasma (Fig. 1i). Acetylcholinesterase positive cells were detected in nearly identical sites as the CSF-contacting neurons. Accordingly, these neurons are considered to be AChE-positive.

The horizontal neurons were seldom seen in the NPO. Their perikarya are spherical in shape, and their thin, bipolar fibers with

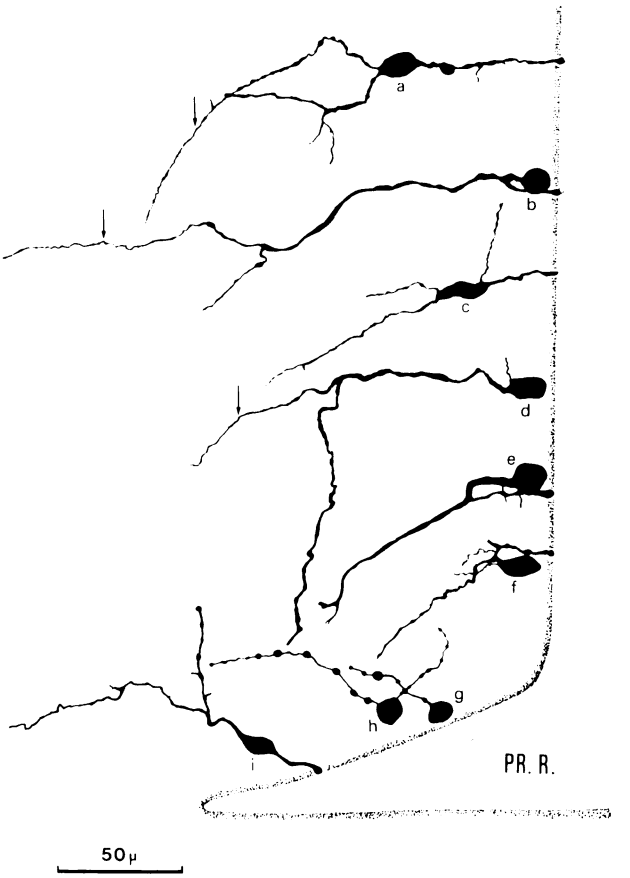

Fig. 1. Drawings of Golgi impregnated cells distributed in a portion of nucleus preopticus. a~f, neurosecretory neurons, arrow indicates the axon emerged from the perikaryon, which may project to the pars nervosa; g and h, horizontal cells; i, CSF-contacting neuron existing just above the chiasma opticorum; PR.R, recessus preopticus.

varicosities projecting run parallel with the ventricular wall (Fig. 1g, h).

The posterior region of the hypothalamus. Three portions were observed in the hypothalamus posterior to the optic chiasma. While the nucleus hypothalami dorsalis (NHD) and nucleus hypothalami ventralis (NHV) are located on the lateral wall of the recessus infundibuli, the nucleus recessi posterioris hypothalami (NRPH) is on the periphery of the recessus posterioris. These two nuclei, NHD and NHV containing almost all neurons, are identified as CSF-contacting neurons (Fig. 2b, c, d, e; Fig. 3). Most of the ventricular processes extending from the perikarya of these neurons have swellings in the middle region, and their collateral fine fibers running parallel to the ventricular wall are seldom seen at the swellings (Fig. 2e).

The apex of the ventricular process forms a bulbous structure, such as the spherule or ovule (Fig. 3). Slender processes with few spines protrude multipolarly from the perikarya to the white matter. It is rather difficult to discriminate the axon from the dendrites in these neurons (Fig. 2a, d, e). The ependymal cells and tanycyte are also encountered in this region. The tanycyte located in the subependymal layer has the bottle-shaped perikaryon, the tip of which faces the ventricle (Fig. 2f). The ependymofugal process of this cell with many fine collaterals appears fluffy.

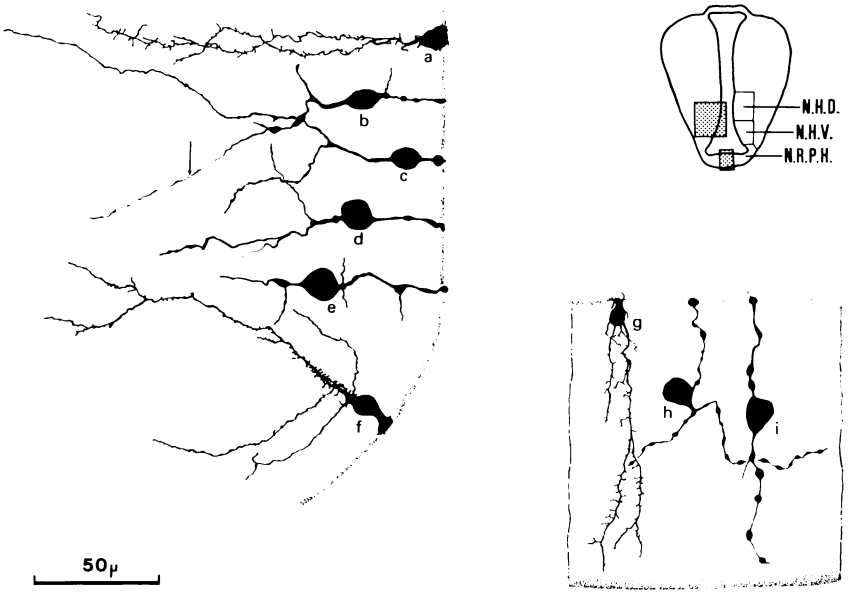

Fig. 2. Drawings of Golgi impregnated cells distributed around the lateral and ventral walls of the recessus infundibuli. a～f, cells located on a large square (dotted); g～i, cells located on a small square (dotted); a, ependymal cell; b～e, CSF-contacting neurons; f and g, tanycytes; h and i, CSF-contacting neurons with varicosities situated on the NRPH; N.H.D., nucleus hypothalami dorsalis; N.H.V., nucleus hypothalami ventralis; N.R.P.H., nucleus recessi posterioris hypothalami.

In the NRPH, the characteristic CSF-contacting neurons are demonstrated (Fig. 2h, i; Fig. 4). The ventricular process with several bulbous swellings similar to varicosities protrude from the perikaryon, and the apex of this process forms a bulbous structure occasionally with a single cilium (Fig. 2i). On the other hand, the process with many varicosities projecting to the ventral side runs near the vental surface of the brain (Fig. 2h; Fig. 4).

In the NRPH, tanycytes bearing the microvilli in their apices are also seen (Fig. 2g). The basal projection of these tanycytes with many minute collaterals projects straight at right angles to the ventricular wall, and reaches the ventral surface. On the way to the surface, the basal projection occasionally sends off two or three branches.

Retrograde axonal transport of HRP. In spite of careful treatment, several specimens failed to reveal any labeled fibers or cells reacting with HRP. In specimens where success was achieved, only the connective tissue between the pars intermedia (or sometimes pars distalis) and the nervous tissue were destroyed. The axonal uptake of HRP was pursued when retrograde transport was successfully achieved.

In a specimen that was kept alive for 4 hours after administration of HRP to the pars nervosa, the cells that reacted positively are demonstrated only in the CSF-contacting neurons distributed in the ventral region of the NHV, but not in the NPO (Fig. 5). If HRP was administered to the nerve fibers of the floor of recessus infundibuli, just above the proximal pars distalis, and the lamprey was kept alive for 4 hours, a reacting substance derived from benzidine was encountered in the extremely limited CSF-contacting neurons just above the administered portion. In specimens kept alive for 10 to 12 hours after administration of HRP to the pars nervosa, the reacting substance was retrogradly transported to some of the neurons, such as the neurosecretory neurons of the NPO, most of the CSF-contacting neurons of the NHV, and

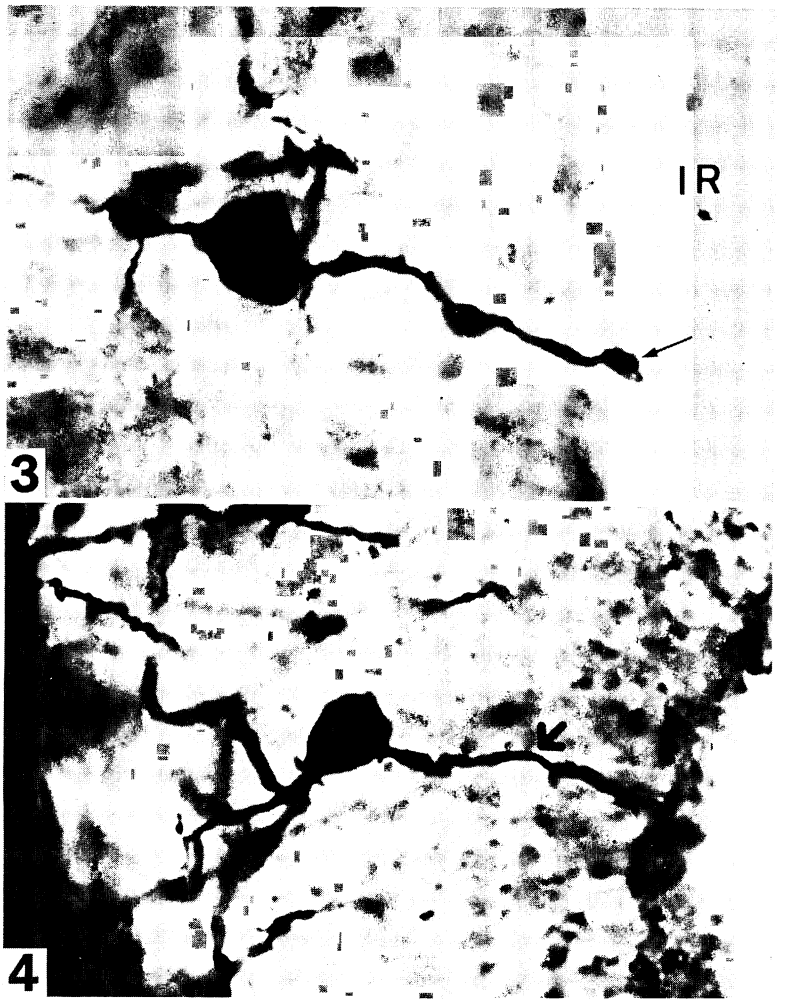

Fig. 3. A Golgi impregnated CSF-contacting neuron with a bulbous structure (arrow) found in the NHV of the lateral wall of the recessus infundibuli. IR, recessus infundibuli. ×850. Fig. 4. A Golgi impregnated CSF-contacting neuron with a ventricular process (arrow) found in the NRPH. ×1,000.

a small number of CSF-contacting neurons of the NHD (Fig. 6). However, such substance was not seen in the ependymal cells and tanycytes.

Discussion

In the NPO of the arctic lamprey, three types of neurons, i.e. the neurosecretory neuron, acetylcholinesterase positive CSF-contacting neuron, and the horizontal cell, were demonstrated by Golgi impregnation. On the other hand, in comparatively primitive actinopterygians, such as *Calamoichthys* and *Anguilla*, six types of cells were described in the preoptic area by Golgi impregnation (Mazzi et al., 1978). The neurosecretory neurons in the NPO of the arctic lamprey is closely similar to the magnocellular neuron in the preopic area of actinopterygians mentioned above. Horizontal cells are commonly seen in the preoptic area of both lamprey and actinopterygians.

The size of perikarya in the neurosecretory neurons of the arctic lamprey is almost equal to each other, and the processes of these neurons usually project bipolarly. The epen-

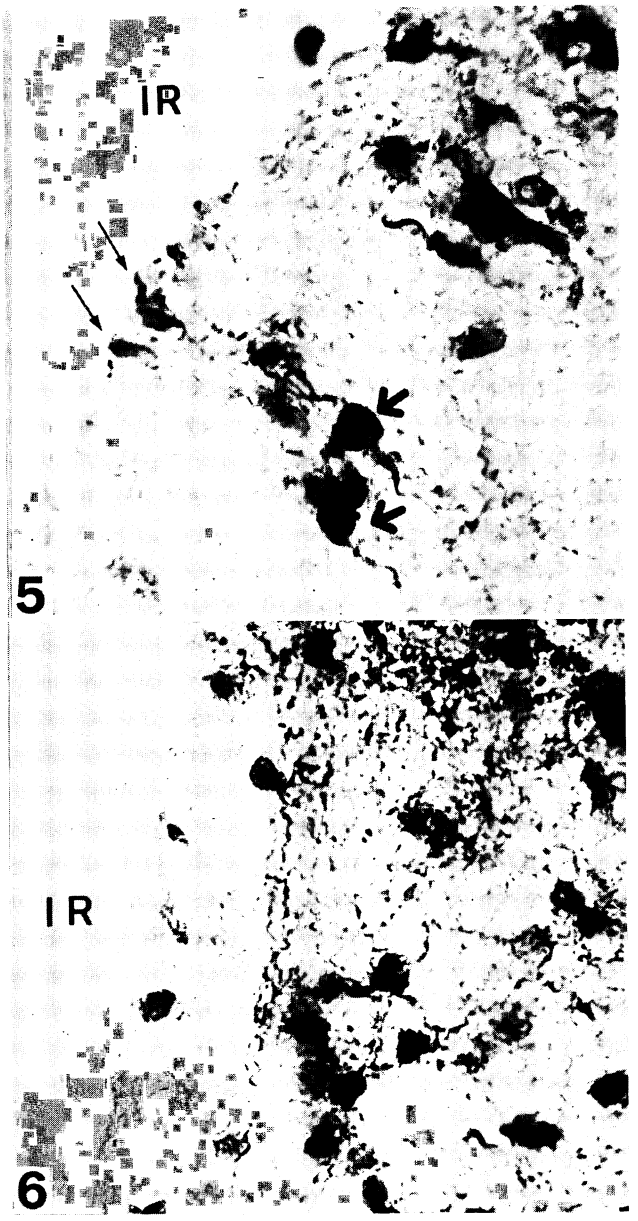

Fig. 5. Labeled CSF-contacting neurons in the NHV 4 hours after administration of HRP. Notice the perikaryon (thick arrows) and the ventricular processes (thin arrows). Cross section. ×530. Fig. 6. Labeled neurons of NHD 10 hours after administration of HRP. Notice HRP-posittive perikarya. IR, recessus infundibuli. Sagittal section. ×300.

dymofugal process of these cells divides into two branches: a thin axon directed to the neurohypophysis and a comparatively thick dendritic process. The dendritic process shows a simple shape, the spine of which is hardly seen. Therefore, these cells may correspond to the "unipolar and bipolar, so-called ependymal type neurosecretory cells" that were recognized by Polenov (1978). The fact that there are many CSF-contacting neurons in the NPO coincides with the result obtained with scanning electron microscopy of the re-

cessus preopticus studied by Shioda et al. (1977) who used the same species as in the present study.

Whether the ventricular process of the neurosecretory neurons is a sensory dendrite or secretory one, that produces and sends the neurohormone to the CSF, can not be ascertained in the present examination of Golgi impregnation. Vigh-Teichmann et al. (1976) reported that the ventricular process of peptidergic CSF-contacting neurons in the preoptic area of teleostean fishes appeared to be the sensory dendrite, based on its fine structure.

By different methods, such as Gomori staining (Öztan and Gorbman, 1960; Sterba, 1972), immunocytochemistry using the antibody on arginine vasotocine (Goossens et al., 1977), and the present examination of retrograde axonal transport of HRP, nearly identical results were obtained in the pathway of fibers from the NPO to the pars nervosa.

With the aid of Falck-Hillarp fluorescence technique, the distribution of biogenic monoamines in the hypothalamic region of the arctic lamprey was first studied by Honma and Honma (1970). All of the monoaminergic cells in the hypothalamus of lower chordates were named the nucleus ependymalis thalami et hypothalami by Baumgarten (1972). Thenceforth, demonstration of monoamines in the lamprey hypothalamus was also achieved by Konstantinova (1973) and Tsuneki et al. (1975). Monoaminergic cells are equivalent to the neuron located on the NRPH and its expansion in an anterodorsal direction, i.e., the lateral wall of the recessus infundibuli. The Golgi impregnated pictures also indicate their presence in these regions. Among others, some characteristic bipolar neurons corresponding to the monoaminergic ones were seen in the NRPH, with their processes bearing the varicosities and bulbous projections. The monoaminergic cells impregnated by the Golgi method have also been reported in the subependymal cells of frog infundibulum (McKenna and Rosenbluth, 1975). However, there is not much similarity between the monoaminergic CSF-contacting neurons located in the NRPH of the arctic lamprey and that of subependymal cell of frogs.

In the hypothalamus of the arctic lamprey, both catecholaminergic and 5-hydroxytryptaminergic cells are demonstrable by improved fluorescence histochemistry (Ochi and Hosoya, 1974). However, it failed to diffferentiate between these cells by impregnated picture alone. To elucidate the detailed morphology of monoaminergic cells, more precise study should be carried out.

Existence of monoaminergic fibers in the pars nervosa of the European river lamprey and the arctic lamprey has been established by fluorescence histochemistry (Baumgarten, 1972; Polenov et al., 1974; Tsuneki et al., 1975). In the case of *Lampetra fluviatilis*, these monoaminergic nerve fibers are considered to originate from the rostral and intermediate portions of the nucleus ependymalis hypothalami (Baumgarten, 1972). The presence of HRP in the CSF-contacting neurons in the lateral wall of the recessus infundibuli just above the pars nervosa that was demonstrated in the present study supports the view made by Baumgarten (1972).

Fiber connection between the pars nervosa and the CSF-contacting neurons situated in the infundibulum is also known in the anuran amphibian (Nakai et al., 1977). Thus, in the arctic lamprey, these CSF-contacting neurons, i.e., the monoaminergic neurons, sending their axons into the pars nervosa, may control the function of the pars intermedia.

It is necessary to determine whether or not the distribution of reacting material of HRP in the hypothalamus of the arctic lamprey is actually derived from retrograde axonal transport. There is a possibility that HRP administered through the pars nervosa flows into the blood canal situated in the boundary between the pars nervosa and the pars intermedia. Thus, by blood stream, HRP may reach the CSF-contacting neuron which connects the capillary to the ventricle, and produce reacting material in such neurons. In the present examination, hardly a case is found in which the CSF-contacting neuron, in contact with the capillary wall, reacts simultaneously to HRP. Accordingly, such a possibility can be ruled out. Another possibility is that the CSF-contacting neuron might absorbe HRP directly from the CSF,

when HRP leaks out through the incision of the ependyma of the pars nervosa and/or the space between the ependymal cells. A careful observation of the present preparation indicated that no scar from injury was encountered anywhere in the ependyma of the pars nervosa. However, reacting material was never detected in either the ependymal cell or the tanycyte which ingested HRP sufficiently from the CSF, even if the specimen was fixed shortly after administration of HRP. Consequently, a distributional map of HRP-reacting material is estimated to be derived from retrograde axonal transport and not by diffusion.

The tanycytes which were first identified and designated by Horstmann (1954) in several species of elasmobranchiate fishes were also seen in the hypothalamus of the arctic lamprey by Golgi silver impregnation. The existence of these cells in the ventricular wall of this species has already been described by Shioda et al. (1977) who studied them by scanning electron microscopy. However, due to a small number of branches and collaterals, the morphology of the lamprey tanycyte is simpler than that of the freshwater teleost, *Leuciscus hakonensis* (Yui and Honma, 1978). Similarly, the shape of the CSF-contacting neuron impregnated in the hypothalamus of the arctic lamprey seems to be simple and primitive in having a comparatively smaller number of branches, and the presence of dendrites with few spines (Ramón-Moliner, 1968).

It is clear that the hypothalamus of the arctic lamprey is mainly occupied by CSF-contacting neurons consisting of various types, i.e. the neurosecretory neuron in the NPO, monoaminergic neuron in the NRPH, and others. Based on the fine structure of the CSF-contacting neurons of many vertebrate species, Vigh and his coworkers considered that the ventricular process corresponds to the sensory dendrite (Vigh and Vigh-Teichmann, 1973; Vigh-Teichmann and Vigh, 1974). Our examination cannot surmise the role of the CSF-contacting neuron. However, it is likely that the major function of these neurons is reception and transmission of information from the CSF to other portions of the brain. Moreover, the CSF-contacting neurosecretory neuron in the NPO may also have a secretory function. Further physiological study is needed to elucidate these assumptions.

Acknowledgments

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ゴルジ渡銀法および HRP の逆行性軸索輸送法によるカワヤツメの視床下部下垂体の観察

油井龍五・本間義治

カワヤツメの視床下部について，ゴルジ渡銀法を用い観察したところ，視束前核が脳脊髄液接触ニューロン (CSF-C ニューロン) に同型の多数の神経分泌ニューロンと，少数の水平細胞から構成されていることが分った．また，視束前核の腹方には，これらとは別な CSF-C ニューロンが存在していた．視床下部後方にある視床下部背方核と視床下部腹方核には，脳室突起をもつ CSF-C ニューロンがみられた．同じく視床下部後方陥凹核には，膨瘤をもつ突起を伸ばしている CSF-C ニューロンが認められた．神経葉に HRP を投与して逆行性に軸索輸送させると，10～12時間後には視束前核の神経分泌ニューロンのほかに，視床下部背方核と視床下部腹方核の CSF-C ニューロン群が標識されていた．上記の結果は，カワヤツメの神経葉が神経分泌性神経線維のほかに，第 III 脳室側壁に存在するモノアミン性 CSF-C ニューロンによって神経支配されていることを示唆している．

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