

Trigeminal and facial innervation of cirri in three teleost species

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Summary. Innervation of the cirri in three teleost species (*Hypsoblennius gilberti*, *Hypsoblennius gentilis*, *Oxylebius pictus*) was investigated with the use of HRP- and cobalt-tracing techniques. All projections were found to be ipsilateral. Labeled cells were demonstrated in both portions of the trigeminal ganglion and in the facial ganglion. Cirrus nerve fibers running in the trigeminal nerve project to terminal fields in an isthmus sensory trigeminal nucleus, to areas adjacent to the descending trigeminal root in the brainstem, and to the medial funicular nucleus in the medulla. Distribution of labeled cells in the trigeminal ganglion complex suggests a functional distinction of the two ganglion portions. Cirrus nerve fibers belonging to the facial nerve terminate in a circumscribed part of the facial lobe, indicating a somatotopic projection. Pathways were principally the same in all three species investigated. Findings of facial innervation of teleost cirri suggest a suspected gustatory function of teleost head appendages.

Key words: Cirri – Trigeminal nerve – Facial nerve – Chemoreception – Teleosts

For the study of chemoreception in vertebrates, fish may be regarded as the most interesting class. Several distinct chemosensory systems have evolved in aquatic animals: the senses of olfaction, of internal taste, of external taste, and a common chemical sense have been differentiated (Schnakenbeck 1960; Bardach and Atema 1971; Bardach and Villars 1974; Finger 1983). Olfaction and external taste were found to serve distance-receptor functions. The spectrum of substances to which both senses respond overlaps significantly; differences with regard to sensitivity are not clear cut (Caprio 1977, 1978).

The number of chemoreceptive senses raises problems of definition, and functional significance, and asks for an explanation of this differentiation within the system of chemoreception.

Answers to this question may be expected, e.g., from

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insights concerning the central interaction of olfaction and taste and the underlying neuronal connectivity.

Materials and methods

Thirty three specimens of *Hypsoblennius gilberti*, Blenniidae, Perciformes (4–10 cm in length), five specimens of *Hypsoblennius gentilis*, Blenniidae, Perciformes (4–10 cm in length), and fifteen specimens of *Oxylebius pictus*, Hexagrammidae, Perciformes (7–20 cm in length), were injected with either HRP (Sigma) or cobalt chloride-lysine (Lazar 1978). Animals were injected into the stump of the cut cirrus (see Fig. 2A) by iontophoresis and/or diffusion for 15–45 min (Springer and Proksch 1982; Schweitzer and Lowe 1984). Specimens were obtained from the California coast near San Diego.

Survival times ranged between 2 and 7 days for the HRP cases and 6 h to 3 days for the cobalt chloride-lysine-injected fish. The fish were anesthetized with tricaine methane sulfonate and perfused through the conus arteriosus with marine teleost Ringer solution (partly containing dissolved H₂S in the cases of cobalt), followed by phosphate buffer, pH 7.4, with 1.5% paraformaldehyde and/or 2.5% glutaraldehyde.

The brains were removed and postfixed in the same fixative. The brains or the decalcified heads were transferred to a 30% sugar solution to avoid freezing artifacts. Sections then were cut in a cryostat at 30–40 µm thickness and picked up on two sets of slides. The HRP sections were reacted with TMB (tetramethylbenzidine) (Warr et al. 1981) or Hanker-Yates reagent (Hanker et al. 1977; Bell et al. 1981) and counterstained with either neutral red and safranin or cresyl violet. The cobalt sections were intensified with Gallyas solution (Gallyas 1979; Schweitzer and Lowe 1984) and counterstained with neutral red and safranin.

Five specimens were used as controls. One fish received an injection of HRP into the skin surrounding the cirrus. Four other specimens of *Hypsoblennius gilberti* were injected into the brainstem with cobalt chloride-lysine. Retrogradely labeled cells in the trigeminal and facial ganglia could be demonstrated in the latter four cases.

Additionally, 38 cirri of *Hypsoblennius gilberti*, 10 cirri of *Hypsoblennius gentilis*, and 19 cirri of *Oxylebius pictus* were investigated with several silver staining methods for demonstration of peripheral nerve endings. Best results were obtained using the Winkelmann method (Winkelmann

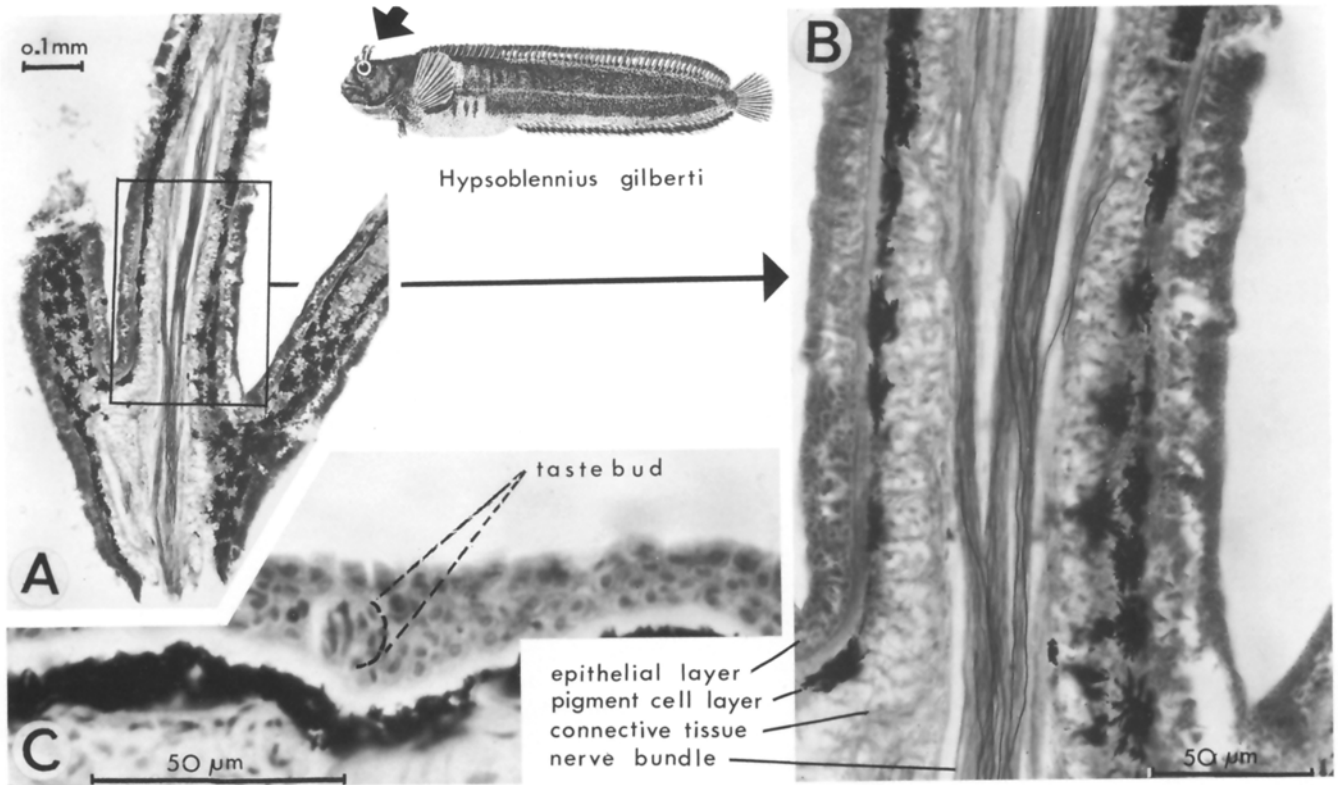


Fig. 1A–C. Longitudinal sections through the cirrus of *Hypsoblennius gilberti*. **A** Section processed with the Winkelmann method for staining of peripheral nerve fibers and counterstained with cresyl violet. **B** Magnification of **A** shows four layers of the cirrus: epithelial layer; pigment cell layer; connective tissue; nerve bundles and blood vessels are located centrally. **C** Cresyl violet-stained section of cirrus “finger” shows taste bud formation in the epithelial layer

1960); some of these sections were lightly counterstained with cresyl violet.

Results

1. *Hypsoblennius gilberti*

a) Periphery. The cirrus of this blenny is shaped like a hand, with a stem and four to six “fingers”. The cirrus consists of four concentric layers: (1) an inner core with blood vessels and nerve bundles, (2) connective tissue, (3) a layer of pigment cells, and (4) an epidermal cell layer with a basal membrane between layers (2) and (3) (see Fig. 1B).

The epidermal cell layer contains taste bud-like formations (see Fig. 1C). Winkelmann silver stainings show peripheral nerves branching in the pigment cell layer with fibers penetrating the basal membrane into the epidermal cell layer. In the center of each cirrus “finger” a centrally located nerve bundle is found. This nerve bundle receives its fibers from the periphery throughout the entire length of the cirrus finger. The nerve bundles of each finger merge in the stem of the cirrus (see Fig. 1A).

b) Pathway. In the tissue above the eye the nerve bundle forms one branch of the supraorbital nerve. Within the supraorbital nerve the cirrus fibers run in five to six bundles which can be traced caudally (see Fig. 2B). The supraorbital nerve runs caudally adjacent to the skull.

On the level of the caudal telencephalon, two portions

of the trigeminal ganglion complex appear. In our experimental specimens both portions contain HRP- or cobalt-labeled ganglion cells. The ganglion located further rostrally consists of smaller cells. Approximately 10–20% of these cells is labeled (see Fig. 2C).

The other ganglion lies slightly further caudally. It contains larger ganglion cells; about 5–10% of this cell population receives cirrus fibers (see Fig. 2D).

Further caudally two distinct fiber bundles can be followed as they gradually shift to the inner side of the skull. Reaching the plane of the optic tectum, the facial ganglion appears. About 20% of these ganglion cells is stained (see Fig. 2E).

It is clearly visible, that the fiber bundles run in two different cranial nerves: the trigeminal and the facial nerve. These can be traced separately as they enter the central nervous system.

c) Central nervous system. The bundle in the facial nerve enters the brain slightly caudal to the entrance of the trigeminal nerve. It courses dorsally; on the level of the most caudal portion of the optic tectum it turns abruptly medially. The fibers almost reach the fourth ventricle; further caudally they terminate in a discrete dorsolateral portion of the facial lobe (see Fig. 2G).

The fibers in the trigeminal nerve run caudally; some of them branch in a position slightly caudal to their entrance into the brain. Branching fibers turn medially and terminate in an isthmus nucleus of the trigeminal nerve (nINV) or “cell group 1” of Luiten (1975); see Fig. 2F.

Further caudally the fibers of the trigeminal nerve form two distinct bundles within the descending trigeminal root (RDV). These two fiber bundles can be traced separately throughout their course in the brainstem. Due to its extremely large diameter one thick nerve fiber can be identified in serial sections. In the brainstem, the one thick fiber and a few others give collaterals to the medial surrounding area throughout their course in the descending trigeminal root (see Fig. 2H).

At the boundary of medulla and spinal cord the fibers turn ventromedially to the nucleus funicularis medialis (nFM) of the trigeminal nerve. Terminations are demonstrated in the nFM, adjacent to the central canal, (see Fig. 2I). All projections were found only on the side ipsilateral to the HRP- or cobalt chloride-lysine injection.

Fig. 3 shows a schematic drawing that summarizes our findings of the innervation of cirri in the blenny.

2. *Hypsoblennius gentilis*

The cirrus of this species is shaped like a Christmas tree. Pathways and central projections of the cirrus-supplying nerve fibers were found to be principally the same in *Hypsoblennius gilberti* and *Hypsoblennius gentilis*.

3. *Oxylebius pictus*

a) *Periphery.* *Oxylebius pictus* possesses two pairs of cirri: one anterior pair is located above the eyes, a second posterior pair is located further caudally on the skull. The anterior pair of cirri is slightly larger than the posterior one. The cirri are shaped similar to those in *Hypsoblennius gilberti* (see Fig. 1A); the stem of the cirrus is larger in *Oxylebius* and the "fingers" are shorter in proportion to the entire cirrus than in *Hypsoblennius gilberti*.

The cirri contain an alcohol-soluble, bright red compound. The stem of the cirrus consists of connective tissue and an epidermal cell layer on the surface. Blood vessels and nerve bundles run mainly through one side of the cirrus stem, not in the center as in *Hypsoblennius gilberti*. Few pigment cells are scattered in an intermediate layer.

b) *Pathway and central nervous system.* The pathway of cirrus nerve fibers to the brain is similar to that described for *Hypsoblennius*. Differences in projections between the anterior and the posterior pair of cirri were not observed. Fibers running to the facial lobe seem more numerous than those coursing in the descending trigeminal root, as compared with *Hypsoblennius*.

Discussion

Initial studies on chemoreception in fish about one hundred years ago had to deal with problems of definition and distinction of taste and smell in aquatic animals (Nagel 1894; Herrick 1908). Sometimes the ability of fish to smell has been denied. The confusion was based on a lack of a definition for smell. Attempts were made to distinguish between olfaction and taste on the basis of thresholds and sensory specificity (Herrick 1904; Parker 1910; Schnakenbeck 1960). Recent investigations (Beidler 1976; Caprio 1977, 1978) rendered evidence for lower thresholds in the taste system as compared with olfaction in certain species. These findings contradict the results of prior investigations.

In recent years our knowledge of receptor morphology and physiological parameters has increased rapidly (Bardach and Atema 1971; Atema 1971; Caprio 1977, 1978). For studies on taste buds in fishes the extremely high concentration of these structures in barbels of catfish have mostly been used (Herrick 1901, 1904; Bardach and Atema 1971; Atema 1971; Reutter 1971; Biedenbach 1973; Grover-Johnson and Farbman 1976; Finger 1976; Caprio 1975, 1977, 1978); the gustatory function in fish does not seem to be necessarily dependent on the existence of a differentiated tastebud formation (Schnakenbeck 1960; Schulte and Holl 1972; Bardach and Villars 1974; Finger 1983).

Taste bud-like structures were described in orbital cirri of *Blennius tentacularis* (Blenniidae, Perciformes), (Schulte and Holl 1972). Teleost head appendages have given rise to speculation on possible sensory functions of these organs (Schulte and Holl 1972; Clark 1984; Rosenblatt, personal communication); their innervation pattern has not previously been studied.

With our study of the innervation of cirri in teleosts we have selectively investigated the innervation pattern of one circumscribed receptive field of the sensory trigeminal and facial nerves. Therefore we can compare our findings with reports on projections of the entire sensory facial and trigeminal nerves; additionally, we report findings concerning the percentage of labeled cells in cranial ganglia, i.e., the relative number of ganglion cells mediating input from this receptive field, and we can answer questions of somatotopic representation in cranial nerve ganglia as well as in the central nervous system.

1. Facial nerve

Studies on taste in fishes have concentrated mainly on two families of teleosts: Ictaluridae and Cyprinidae. Both are families with a highly developed and extremely specialized sense of (external) taste. This is reflected by the extension of the gustatory (facial) lobes of catfish and cyprinid brains (see Fig. 4).

Projections of the facial nerve have been traced with modern neuroanatomical methods in both families (catfish: Finger 1976, 1978, 1983; carp: Luiten 1975; goldfish: Morita 1980). The pathway of the facial nerve seems to be principally the same in *Ictalurus*, *Carpinus*, *Carassius*, and our investigated species *Hypsoblennius* and *Oxylebius*. In the studies on carp and goldfish no findings concerning the ganglia have been reported.

The gustatory specialists, Ictaluridae and Cyprinidae, differ extremely with regard to the respective form and size of their facial lobe, and when compared with a "normal" teleost brain (see Fig. 4). *Hypsoblennius* (Blenniidae) and *Oxylebius* (Hexagrammidae) possess a paired facial "lobe" or equivalent of the facial lobe, while Cyprinidae have a central, unpaired facial lobe which is about five times larger in proportion (see Fig. 4).

Remarkable is the apparent somatotopic representation in the facial lobe, which the data suggest to be present (see facial lobe of *Hypsoblennius gilberti* in Fig. 2G); somatotopy is not apparent in the facial ganglion (Fig. 2E). The existence of a somatotopic gustatory representation in the catfish facial lobe is controversial (Biedenbach 1973; Finger 1976, 1978, 1983). Our findings are in accordance with Finger's results of somatotopic gustatory projections.

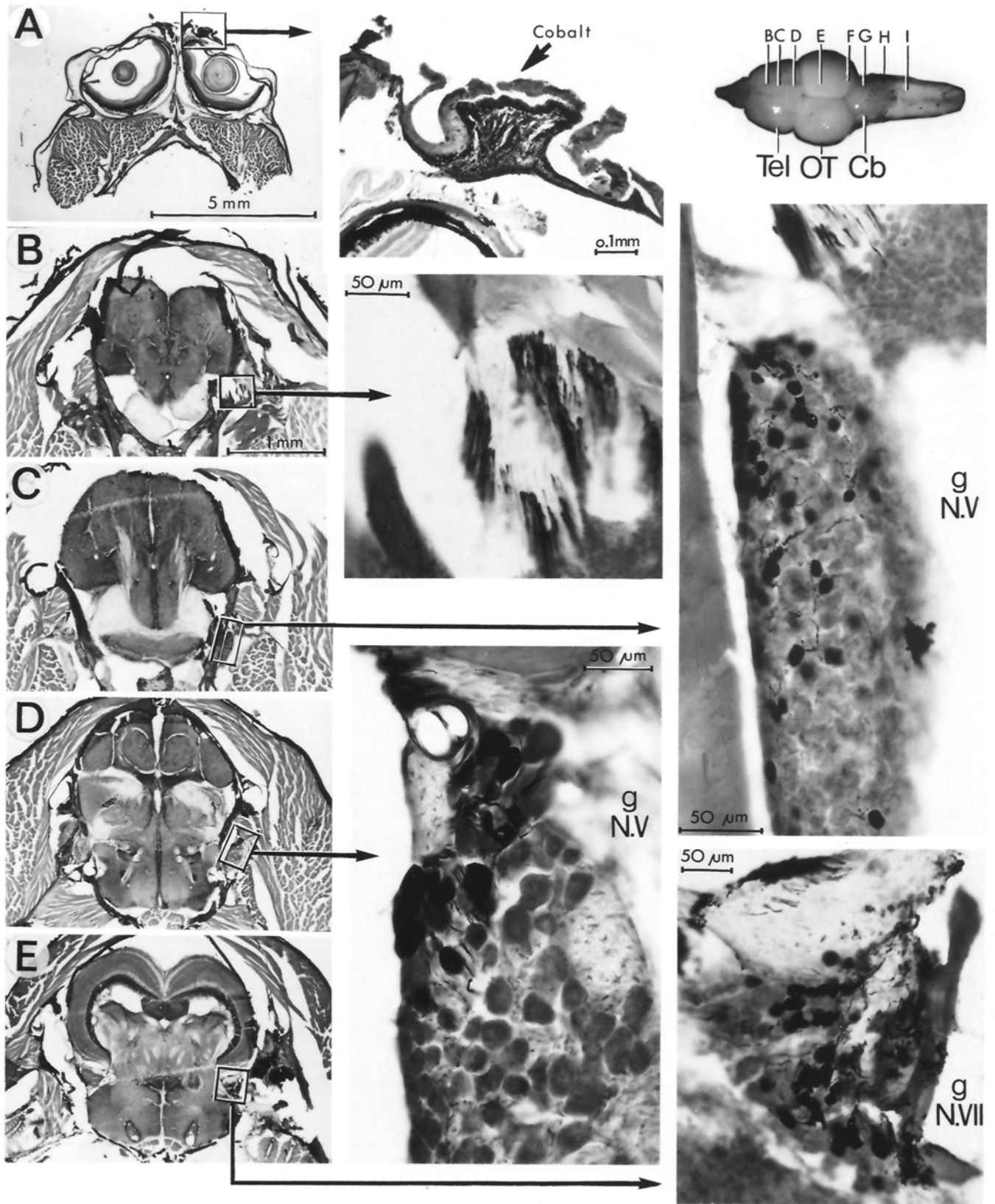


Fig. 2A-E.

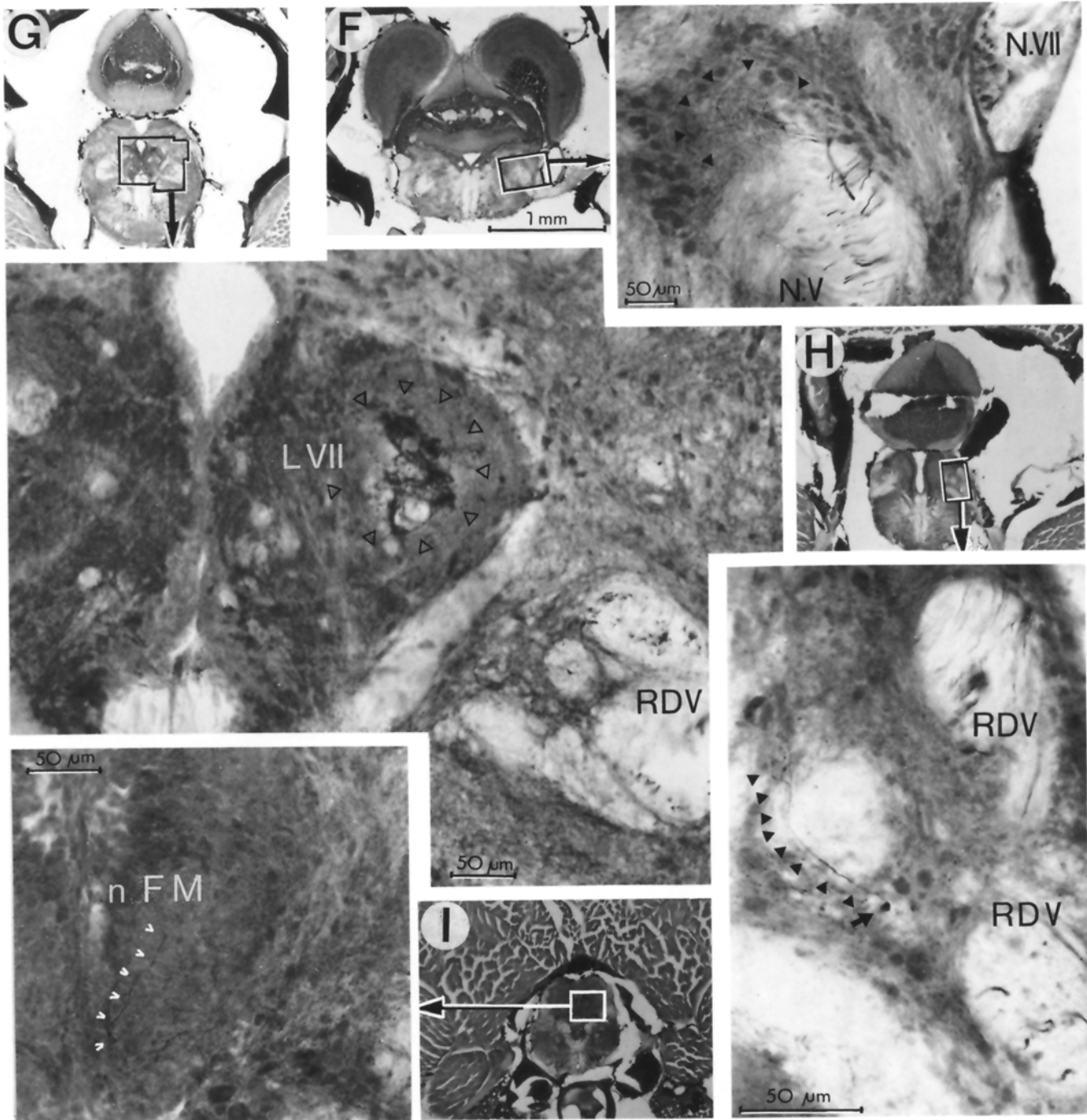


Fig. 2A-I. Frontal sections through the head of *Hypsoblennius gilberti* after application of cobalt chloride-lysine to the stump of the cut cirrus. All sections belong to one specimen. **A** is most rostral, **I** is most caudal. The dorsal view of the *Hypsoblennius* brain (next to section **A**) indicates levels of sections **B** to **I**. *Tel* telencephalon; *OT* optic tectum; *Cb* cerebellum. **A** Level of eyes and cut cirrus; higher magnification shows the cirrus stump. *Arrow* demonstrates location of applied cobalt chloride-lysine during injection. **B** Level of rostral telencephalon; higher magnification shows five fascicles in the combined anterior branch of the trigeminal and facial nerve. **C** Level of caudal telencephalon; higher magnification shows the rostral portion of the trigeminal ganglion (*g N.V*) containing small-sized ganglion cells. Approximately 15% of this cell population is labeled with cobalt. Labeled cells are scattered, somatotopy is not apparent. **D** Level of diencephalon; higher magnification of the caudal portion of the trigeminal ganglion (*g N.V*) containing large-sized ganglion cells. Approximately 5 to 10% of this cell population is labeled with cobalt. Somatotopic representation is clearly visible. **E** Level of optic tectum; higher magnification of the facial ganglion (*g N.VII*). Approximately 15 to 20% of this cell population is labeled with cobalt. **F** Level of caudal optic tectum; high magnification shows terminations (*triangles*) in an isthmus nucleus of the trigeminal nerve (*nINV*). This nucleus is located dorsomedially to the trigeminal nerve (*N.V*) and ventrally to the secondary gustatory nucleus. The facial nerve (*N.VII*) is about to enter the central nervous system at this level. **G** Level of facial lobes; higher magnification shows terminal field in a circumscribed portion of the facial lobe (*LVII*), (*arrowheads*); demonstrating somatotopic gustatory projection. The descending trigeminal root (*RDV*), located ventrolateral to the facial lobe, is not yet divided into two fascicles at this level (compare with Fig. 2H). **H** Level of cerebellum; high magnification shows two fascicles of the descending trigeminal root (*RDV*). One large diameter fiber (*arrow*) lying medially to the *RDV* is sending one collateral (*triangles*) into dorsomedial direction. **I** Level of caudal medulla/spinal cord; high magnification shows terminations (*arrowheads*) of the descending trigeminal root (*RDV*) in the nucleus funicularis medialis (*nFM*)

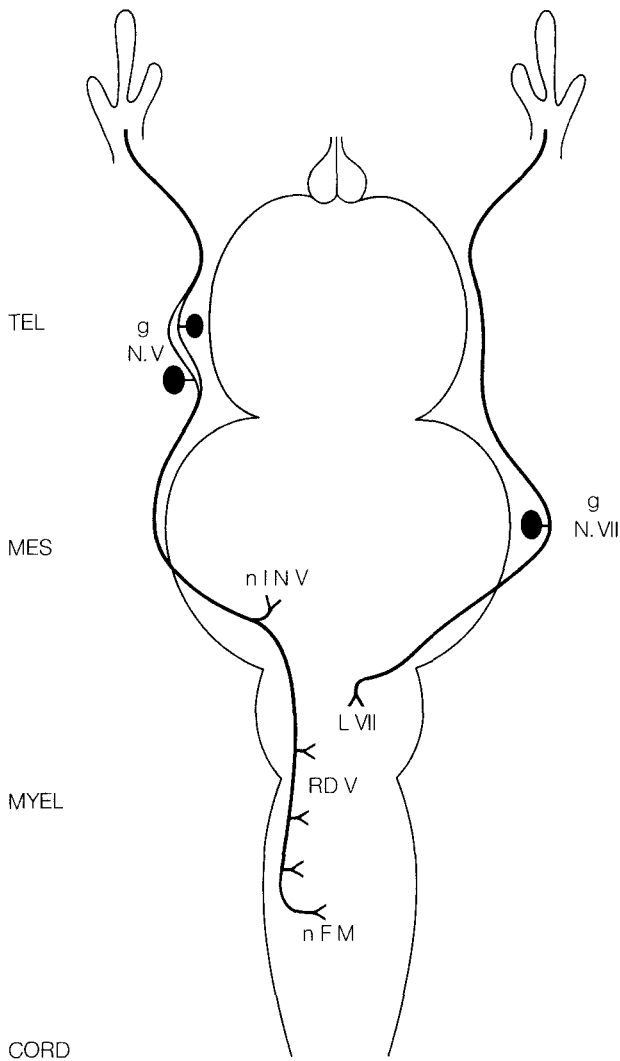


Fig. 3. Schematic drawing summarizes findings of trigeminal (*left*) and facial (*right*) innervation of teleost cirri. Terminal fields of the trigeminal nerve are distributed throughout the course of the descending trigeminal root (RDV) in the myelencephalon (MYEL). Difference in cell size within the two portions of the trigeminal ganglion complex (*g N.V.*) is reflected by drawings. *nINV* isthmic nucleus of the trigeminal nerve; *nFM* nucleus funicularis medialis; *g N.VII* ganglion of the facial nerve; *L.VII* facial lobe

2. Trigeminal nerve

To our knowledge there are no reports of tracer studies on circumscribed receptive fields of the trigeminal nerve in teleosts. Luiten (1975) investigated the projection of the entire trigeminal nerve in the carp with degeneration methods, without giving any information on the distribution of ganglion cells in the trigeminal ganglia. Our findings of trigeminal terminal fields are in accordance with Luiten's (1975) report on the carp.

In most vertebrates the original dual trigeminal ganglia fuse during ontogenetic development (van Wijhe 1883; van Valkenburg 1911). One division is believed to be an ophthalmic, the other a maxillo-mandibular division (van Valkenburg 1911; Molenaar 1978b). In a few vertebrates, some teleosts and reptiles, these two divisions of the trigeminal ganglia remain separated during ontogeny (Hoffmann

1890; Scharf 1958; Molenaar 1978b). Our findings show that *Hypsoblennius* belongs to the latter group; Two distinct trigeminal ganglia can be demonstrated, *both* are involved in cirrus innervation.

These findings and the clear difference of cell size in both ganglion portions give reason to believe that the significance of the two trigeminal ganglia may lie in a functional difference (e.g., different modalities: pain, touch, temperature- or vibration perception) rather than in a gross somatotopic differentiation as known from the ophthalmic, maxillary and mandibular divisions of the trigeminal nerve in higher vertebrates (Kerr 1963; Darian-Smith 1973; Liebermann 1976). In a study of single unit recordings of the trigeminal ganglion in mammals no clustering of sensory modalities was found (Kerr and Lysak 1964).

In our study we noted that only one of the two trigeminal ganglia of *Hypsoblennius*, the ganglion portion containing large-sized cells, appears to be organized somatotopically (see Fig. 2D).

An interesting question is whether the two ganglion portions possess different projections in the central nervous system. This question cannot be answered at present; it has to be kept in mind, however, that the descending trigeminal root (RDV) is divided into two distinct fascicles on its way through the brainstem in *Hypsoblennius* (see Fig. 2H). A division of the descending trigeminal root was first mentioned by van Valkenburg (1911). He described a dorsal and ventral (ophthalmic and maxillo-mandibular) division in some species: teleosts, amphibians, reptiles (van Valkenburg 1911; Woodburne 1936; Crosby and Yoss 1954).

Our findings concerning the termination of primary afferent trigeminal fibers throughout the entire length of the descending trigeminal root (RDV) confirm earlier reports (Woodburne 1936; Nieuwenhuys and Pouwels 1983). It should be mentioned that most of the fibers that project to the isthmic nucleus of the trigeminal nerve (*nINV*) (cell group 1 of Luiten 1975) seem to be collaterals of fibers forming the RDV. This branching of fibers has not been considered in previous reports on teleosts (Nieuwenhuys and Pouwels 1983).

A classification of trigeminal fiber pathways in vertebrates has been provided by Windle (1926). He differentiated three types: (1) (proximal) unbranched descending, (2) bifurcating, (3) non-bifurcating ascending fibers; and he correlated these fiber types with different functions: (1) pain reception, (2) temperature and tactile perception, (3) discriminatory types of tactile stimuli (Windle 1926; Crosby and Yoss 1954). Fiber type (3) is assumed to be present only in higher submammals and in mammals. Concerning trigeminal projections in teleosts our findings are in accordance with the suggested fiber classification.

In some reptiles (snakes) a special sense of infrared perception is part of the trigeminal sensory system, forming an anatomically and functionally separated portion within this sensory apparatus (Molenaar 1978a, b). Possibly teleost cirri and reptile infrared-reception can be considered specialized trigeminal subsystems with differentiated central pathways, which can be distinguished from those of ordinary cutaneous perception.

3. Correlation between different chemosensory modalities

Our findings of facial and trigeminal cirrus innervation support Herrick's (1901) theory of coinnervation of identical

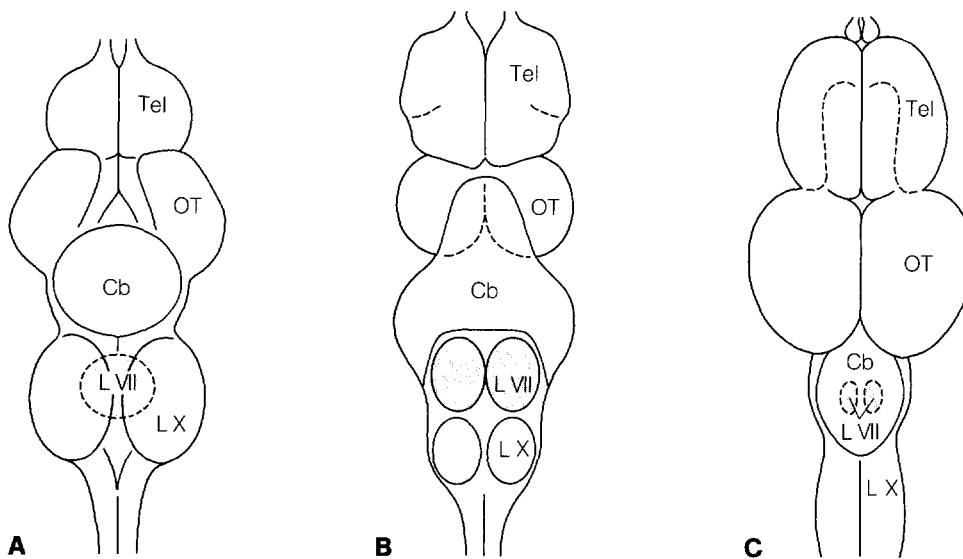


Fig. 4. A–C Schematic drawings of dorsal views of teleostean brains. *Gray areas:* Facial lobes (L VII); *Cb* cerebellum, *LX* vagal lobe, *OT* optic tectum, *Tel* telencephalon. **A** Brain of *Carassius*; **B** brain of *Ictalurus*; **C** brain of *Hypsoblennius*. For reasons of comparison, brains are drawn to same size. Note the variety of proportional size and form of the facial lobes

skin areas by these two nerves (Herrick 1901, 1905, 1906). Ariëns-Kappers et al. (1936) reported that tactile innervation is necessary for the elicitation of gustatory responses in fish. It is remarkable in this context that the most rostral terminal field of the trigeminal nerve, the isthmic nucleus (nIN), is located adjacent to the secondary gustatory nucleus, and that secondary facial projections reach the nucleus funicularis medialis (nFM), a primary projection area of the trigeminal nerve (Herrick 1905, 1906; Finger 1976, 1978). Correlation of gustatory and tactile input could easily be mediated by these pathways.

Further points of interest concern olfactory-gustatory interaction. Findings that identical substances and similar realms of concentrations stimulate olfaction as well as taste (Beidler 1976; Caprio 1977, 1978) show that the difference of behavior due to taste and smell, respectively, is to be found in the difference of the connectivity and central processing of peripherally identical information (Herrick 1908; Bardach and Atema 1971).

In unpublished preliminary studies on goldfish we have found efferents to the olfactory bulb to originate from an isthmic region located in the vicinity of the isthmic trigeminal field. Further studies will attempt to clarify whether afferents mediated by the fifth or seventh nerve do exert a modulatory influence on olfactory perception.

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