THE
PHYSIOLOGY
OF FISHES
Second Edition

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11 The Central Nervous System

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I. INTRODUCTION

"Fishes" are a prime textbook example for a nonmonophyletic group because they include animals such as *Latimeria* and lungfishes, which represent the closest outgroups of tetrapods, and also creatures such as hagfishes (Myxinoidea) which are not even vertebrates (Figure 1A). A recent comparative discussion of the central nervous system (CNS) of all fish taxa is provided by Butler and Hodos[41] and further information on the nervous systems of hagfishes and lampreys can be found in Northcutt[179] and Wicht and Northcutt,[230] of cartilaginous fishes in Northcutt[174] and Smeets et al.,[219] of teleosts in Wullimann et al.,[244] and of lungfishes and coelacanths in Northcutt[180] and Northcutt and Bemis.[183] Here, a survey on the bauplan of the fish CNS and the connectional organization (hodology) of sensory, motor, and integrative centers will be given in order to provide a functional neuroanatomical basis for other chapters. The emphasis is on teleosts, but reference to other taxa will be made in appropriate contexts and in the final comparative section. The neuroanatomical terminology is according to Wullimann et al.[244]

A. THE BAUPLAN OF THE FISH CENTRAL NERVOUS SYSTEM

Conventionally, the vertebrate brain is divided into five parts which, from rostral to caudal, are the telencephalon and the diencephalon (together representing the forebrain), the mesencephalon, the metencephalon (including the cerebellum and pons), and the myelencephalon. Traditional embryology describes that the vertebrate brain develops from a three-vesicle stage exhibiting a most caudal, rhombencephalic vesicle (including metencephalon and myelencephalon), a mesencephalic vesicle, and a most rostral prosencephalic vesicle (including diencephalon and telencephalon) into a five-vesicle stage (representing the primordia of the five adult brain parts mentioned above).

Recently, theories on the neuromeric organization of the vertebrate brain have seen an renaissance. Cytological and molecular-genetic studies suggest that the vertebrate rhombencephalon develops from seven or eight transitory neuromeres (rhombomeres), and that the prosencephalon does so from six more neuromeres (prosomeres[195,244]). Such findings challenge the traditional concept of brain subdivision. Even from a comparative anatomical viewpoint, the division of the rhombencephalon (hindbrain) into metencephalon and myelencephalon appears questionable in anamniotes. With the exception of the cerebellum, the ventral (medullary) remainder of the metencephalon can be separated only arbitrarily from the more caudal myelencephalic portion of the medulla oblongata (Figure 2). Thus, it makes more sense to treat cerebellum and medulla oblongata as entities.[244] Medulla oblongata and the ventral part of the mesencephalon, the tegmentum (see below), are collectively referred to as brainstem here (a usage distinctly different from that of human neurology, where optic tectum and even diencephalon are also considered part of the brainstem).

A

CRANIATA

VERTEBRATA

GNATHOSTOMATA

SARCOPTERYGII

TETRAPODA

AMNIOTA

MYXINOIDEA
(HAGFISHES)

PETROMYZONTIDA
(LAMPREYS)

CHONDRICHTHYES
(CARTILAGINOUS FISHES)

ACTINOPTERYGII
(RAY-FINNED FISHES)

ACTINISTIA
(LATIMERIA)

DIPNOI
(LUNGFISHES)

AMPHIBIA

MAMMALIA

SAUROPSIDA

B

ACTINOPTERYGII

ACTINOPTERI

NEOPTERYGII

HALECOSTOMI

TELEOSTEI

OSTEOGLOSSOMORPHA

ELOPOMORPHA

CLUPEOCEPHALA

CLUPEOMORPHA

EUTELEOSTEI

NEOTELEOSTEI

ACANTHOMORPHA

ACANTHOPTERYGII

CLADISTIA
(POLYPTERUS)

CHONDROSTEI
(SCAPHIRHYNCHUS)

GINGLYMODI
(LEPISOSTEUS)

HALECOMORPHI
(AMIA)

OSTEOGLOSSOIDEI
NOTOPTEROIDEA
HIODONTIDAE

ELOPIDAE
MEGALOPIDAE
ANGUILLIFORMES

CLUPEOIDEI
DENTICIPITOIDEI

ESOCAE

OSTARIOPHYSI
OSMEROIDEI
ARGENTINOIDEI

SALMONIDAE

STOMIIFORMES

AULOPIFORMES

MYCTOPHIFORMES

PARACANTHOPTERYGII

ATHERINOMORPHA

PERCOMORPHA

FIGURE 1. Cladograms show systematic relationships of recent taxa of (A) craniates and (B) ray-finned fishes (Actinopterygii). (After Lauder, G. V. and Liem, K. F., *Bull. Mus. Comp. Zool. Harv. Univ.*, 150, 95, 1983.)
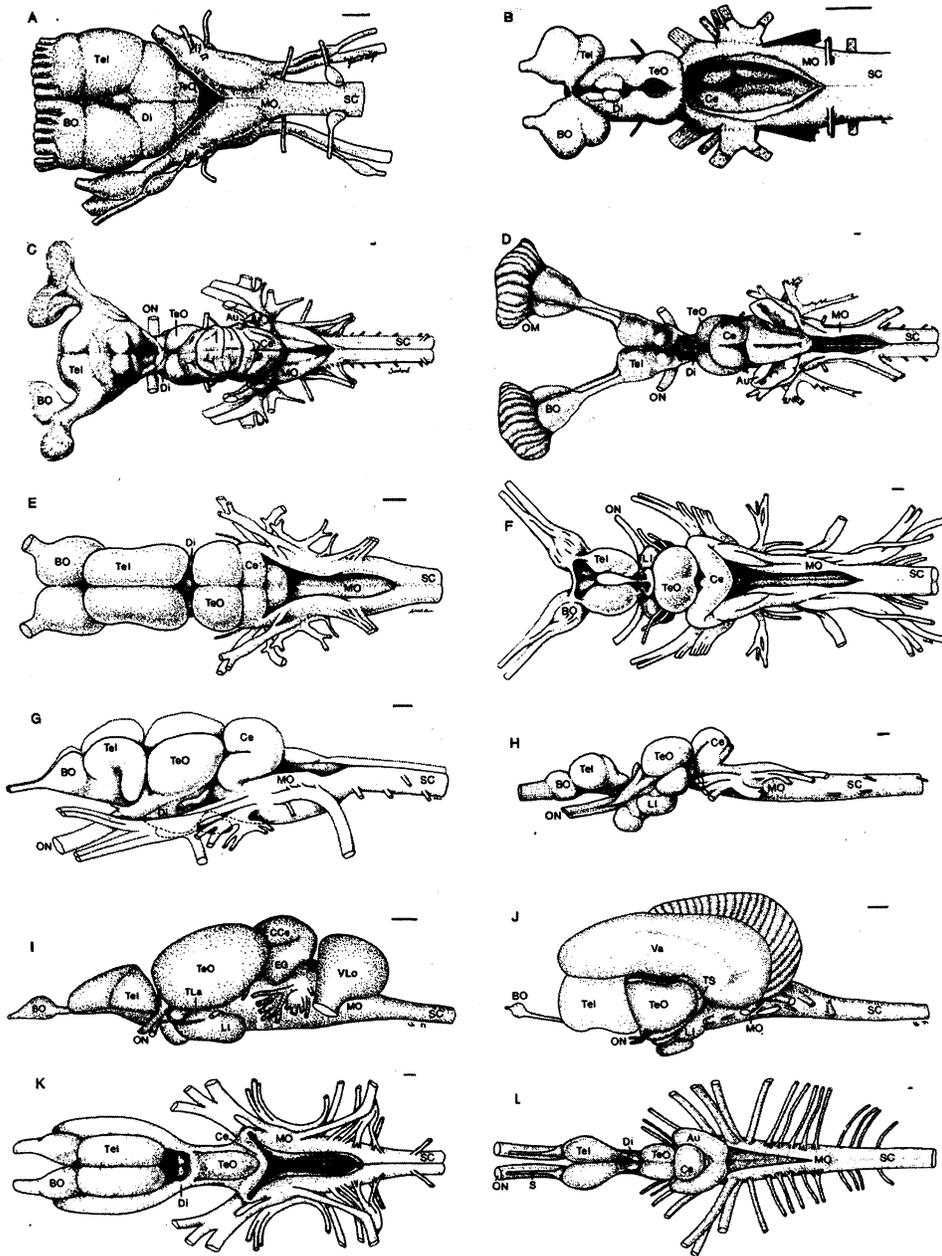
FIGURE 2. Lateral or dorsal views of various fish brains. (A) *Eptatretus stouti* (Pacific hagfish), (B) *Ichthyomyzon unicuspis* (silver lamprey), (C) *Mustelus canis* (smooth dogfish), (D) *Squalus acanthias* (spiny dogfish), (E) *Polypterus palmas* (bichir), (F) *Scaphirhynchus platorynchus* (shovelnose sturgeon), (G) *Lepisosteus osseus* (longnose gar), (H) *Amia calva* (bowfin), (I) *Carassius auratus* (goldfish), (J) *Gnathonemus petersi* (mormyrid), (K) *Protopterus annectens* (African lungfish), (L) *Latimeria chalumnae* (coelacanth). Scale bars: 1 mm. Some drawings courtesy of R. Glenn Northcutt (B–H,K,L) and Helmut Wicht (A). Rostral is to the left in Figures 2 to 13. For all abbreviations, see list.

The mesencephalon of all fishes includes a dorsal optic tectum and a ventral tegmentum. The term *tegmentum* is ambiguous. In mammals, the roof of the mesencephalon (tectum mesencephali) consists of the superior colliculus (tectum opticum of other vertebrates, part of the visual system) and the inferior colliculus (torus semicircularis of other vertebrates, part of the auditory system). The ventral mesencephalon is separated from this roof by the ventricle and forms the tegmentum, which has a dominant role in motor functions. The tegmentum arises embryonically from the basal plate in contrast to the alar plate-derived, sensory-related tectum opticum and torus semicircularis. Here, the term *tegmentum* shall be used strictly in this embryologically justified sense. However, since the adult torus semicircularis comes to lie on top of the tegmentum in many anamniotes, it is sometimes considered part of the tegmentum (see Reference 173).

Classically, the diencephalon has been described in dorsoventral order to consist of the epithalamus, the dorsal thalamus, the ventral thalamus, the posterior tuberculum, and the hypothalamus. The preoptic area (often considered part of the hypothalamus) is considered here an intermediate region between telencephalon and diencephalon. Furthermore, the pretectum is intricately intermingled with diencephalic cell groups. The neuromeric model[195] proposes that the classical diencephalic vesicle includes two prosomeres (P1,P2); the one adjacent to the mesencephalon giving rise to all of the pretectum, the second one developing into epithalamus and dorsal thalamus. Of the four more rostral prosomeres, P3 gives rise to the ventral thalamus, and the telencephalon and hypothalamus are derived from the dorsal and ventral parts, respectively, of P4 to P6 (the secondary prosencephalon). The posterior tuberculum develops from the ventral portions of prosomeres 1 to 3. Thus, diencephalon and telencephalon gain a new meaning in this model, since the classical dorsoventral order of diencephalic divisions turns into a caudorostral sequence and the telencephalon as well as the hypothalamus are part of the same prosomeres.

B.   THE COMPARATIVE METHOD

Since the evolutionary interpretations in this analysis follow cladistic methodology[90] some of its basic terms and concepts shall be introduced. One of its important premises is that not whole recent organisms but the single characters that they display (such as nuclei, neuronal connections, neurotransmitter distribution) are ancestral (plesiomorphic) or derived (apomorphic). Well-supported cladograms (Figure 1) serve as a basis for the evolutionary interpretation of the distribution of neural characters here. Cladograms are hypotheses on the systematic relationship of organisms and are exclusively based on shared derived characters (synapomorphies). Sistergroups are two taxa (e.g. sarcopterygians-actinopterygians in Figure 1A) characterized by certain synapomorphies which they inherited from their last common ancestor separating them from the outgroup taxa (e.g., cartilaginous fishes in Figure 1A). Cladograms help in the determination of evolutionary polarity (plesiomorphy vs. apomorphy) of particular neural characters through application of the outgroup comparison. If two conditions of a neural character occur in sistergroups (presence of palliospinal tract in some sarcopterygians, absence in actinopterygians), the condition in the outgroups is investigated (absence of palliospinal tract in cartilaginous fishes). Using parsimony (principle of choosing the simplest explanation), the condition in the outgroup is considered to represent the plesiomorphic condition.

II.   FUNCTIONAL ANATOMY OF THE TELEOSTEAN BRAIN

Most basic to an understanding of functional neuroanatomy are neuronal connections in the CNS. Here, exclusively, connections established with experimental neuronal tracing or

with degeneration experiments are considered. In general, connections are ipsilateral (i.e., they do not cross the CNS-midline), unless otherwise mentioned.

A. SENSORY SYSTEMS
1. Olfaction

As in all vertebrates, the only primary sensory receptor cells in teleosts are located in the olfactory mucosa, i.e., the axons of these cells represent the primary olfactory projections (fila olfactoria, olfactory nerve) and reach the glomerular layer of the olfactory bulbs.[172] The number of glomeruli per olfactory bulb in adult teleosts ranges between 80 in the adult zebrafish (22 of which are intraspecifically individually identifiable[5]) and several hundreds in larger species. In the rainbow trout *Oncorhynchus mykiss* (formerly *Salmo gairdneri*), olfactory receptor cells that project to a specific glomerulus are distributed evenly all over the olfactory mucosa and they probably terminate exclusively in one glomerulus.[201] Molecular studies in the catfish *Ictalurus punctatus* show that a specific olfactory receptor cell has only a few receptor types.[168] Furthermore, olfactory receptor cells characterized by such a limited set of receptor types are distributed evenly all over the mucosa.[169] Thus, if each set of evenly distributed sensory cells characterized by few receptor types were to be identical to one set of sensory cells projecting to a single glomerulus, a particular olfactory glomerulus would process olfactory information derived from only very few (or one) receptor types.

Another cranial nerve, the terminal nerve, runs together with the olfactory nerve. In most teleosts, the terminal nerve ganglion cells lie in or near the ventral olfactory bulb. These ganglion cells have a peripheral dendrite which sometimes reaches into the olfactory mucosa and a central axon which always projects beyond the olfactory bulbs into the ventral telencephalon, preoptic region, or contralateral retina.[8] The functional significance of the terminal nerve is not entirely clear, although there is good evidence that it may be involved in pheromone detection and in mediating sexual behavior such as sperm release.[48,49,53] It has been claimed repeatedly that primary olfactory projections — in addition to terminal nerve projections — reach the CNS beyond the olfactory bulb.[14,93,94,202] However, only recently were olfactory receptor cell bodies documented in the mucosa of the trout *Salmo trutta* to project to the hypothalamus.[3]

The teleostean secondary olfactory projections originate in the large mitral cells of the olfactory bulb and run in the lateral and medial olfactory tracts. While the medial olfactory tract (which includes the terminal nerve fibers) appears to carry information related to sexual behavior, the lateral olfactory tract mediates feeding behavior and alerting responses.[82] Secondary olfactory projections in teleosts are ipsilateral (with a small contralateral component) and reach most nuclei in the area ventralis telencephali, a caudal ventrolateral part of the area dorsalis telencephali, as well as the preoptic and posterior tubercular regions of the diencephalon.[172,210] In the goldfish *Carassius auratus*[10,125] the most dense secondary olfactory terminals within the ventral telencephalic area are located in the central, ventral, and dorsal nuclei, while in the dorsal telencephalic area the posterior zone and nucleus taeniae are the major recipients (Figure 3). Secondary olfactory terminals are also found in the anterior preoptic region and the posterior tuberal nucleus of the goldfish diencephalon. The olfactory bulb, in turn, receives projections from the secondary olfactory (and additional) centers in the telencephalon. Very similar connections of the olfactory bulb are seen in *Ictalurus punctatus*,[11,12] where additional interbulbar connections exist. The dorsal zone of area dorsalis telencephali in the goldfish[190] as well as the ventromedial part of the medial zone of area dorsali telencephali in *Sebastiscus marmoratus*[163] have been described as tertiary olfactory targets, since both regions receive projections from the posterior zone of area dorsalis telencephali and from nucleus taeniae. A second tertiary olfactory region within area dorsalis telencephali (goldfish: caudal part of Dm,[190] *Sebastiscus*: dorsolateral part of Dm[163]) receives ascending projections from the diencephalic (secondary olfactory) posterior tuberal nucleus (Figure 3).
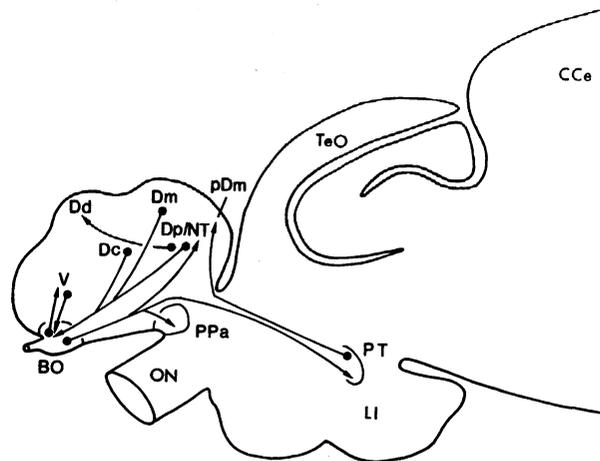
FIGURE 3. Olfactory pathways in cyprinids.[10-12,125,190,210] Figures 3 to 13 represent schematic sagittal sections which show the origins (filled or empty circles) and targets (arrowheads) of central nervous connections (arrows).

2. Vision

Most teleosts are highly visually guided animals and some of their capabilities involving this sensory modality are impressive,[51] e.g., presence of four cone types and tetrachromacy in goldfish color vision,[167] or maintenance of size and color constancy of objects.[52] While the retinotectal system always forms the predominant teleostean visual subsystem, there is great variability in the degree of differentiation of other visual subsystems (e.g., pretectum), indicating substantial functional differences in the visual system of various teleostean taxa.[188,243]

In contrast to other sensory nerves and most sensory organs which are embryonic derivatives of neural crest and placodes, the retina and optic nerve are embryonically derived from the neural tube and, thus, constitute part of the CNS. Despite the fact that multisynaptic processing of visual information occurs in the retina already, the axons of the retinal ganglion cells are conventionally designated as primary retinal projections. As in other vertebrates, five major central nervous areas receive primary retinal input (mostly contralaterally) in teleosts: (1) the optic tectum, (2) the thalamus, (3) the pretectum, (4) the accessory optic system, and (5) the preoptic area.[188]

The ganglion cells of the retina project topographically onto the contralateral tectum where they form several bands of terminals.[9] In the goldfish,[146,178] the most peripheral retinal fibers are located in the superficial white and gray zone; a thin band is located in layer 14 (sometimes referred to as "stratum opticum"), and a much thicker band in layers 8 to 12. A third band of retinal input is seen at the boundary zone between layers 5 and 6 within the central zone, and a fourth band is present in layer 4 within the deep white zone. While the teleostean optic tectum is not exclusively a visual structure, it is unquestionably the major visual center in the teleostean brain where information concerning movement, shape, and color of objects are analyzed.[52,81,147]

Distinct large retinal terminal fields are also present in the thalamus, lateral to the anterior, intermediate, and ventrolateral/ventromedial thalamic nuclei, and the dendrites of these thalamic nuclei reach into the retinal terminal fields. Unfortunately, little is known on the physiology of the thalamic visual centers.[212] Single-cell recordings demonstrate that (dorsal and ventral) thalamic neurons have relatively large receptive fields (approximately 20°), that they are best stimulated by stationary visual cues, and that they do not respond to direction and do not habituate.[74] Bimodal neurons (visual-somatosensory) are present in the ventral,

but not in the dorsal thalamus.[74] Similar to tetrapods, two higher-order visual pathways to the telencephalon arise in the teleostean dorsal thalamus (Figure 4A), one via the anterior thalamic and a second one via the dorsal posterior thalamic nucleus.[59] The anterior thalamic nucleus is a primary retinal target and the dorsal posterior thalamic nucleus is in receipt of tectal input (Figure 4A). Thus, the pathways ascending from these two dorsal thalamic nuclei to the telencephalon resemble the geniculate and extrageniculate visual systems of mammals and their homologues in other tetrapods. However, the telencephalic targets of these dorsal thalamic nuclei are reported by Echteler and Saidel[59] to be the lateral and medial zones of area dorsalis telencephali. This remains controversial, since neither Murakami et al.[163] in *Sebastiscus marmoratus* nor Wullimann and Meyer[235] in the goldfish reported ascending telencephalic projections to the area dorsalis originating in these dorsal thalamic nuclei.
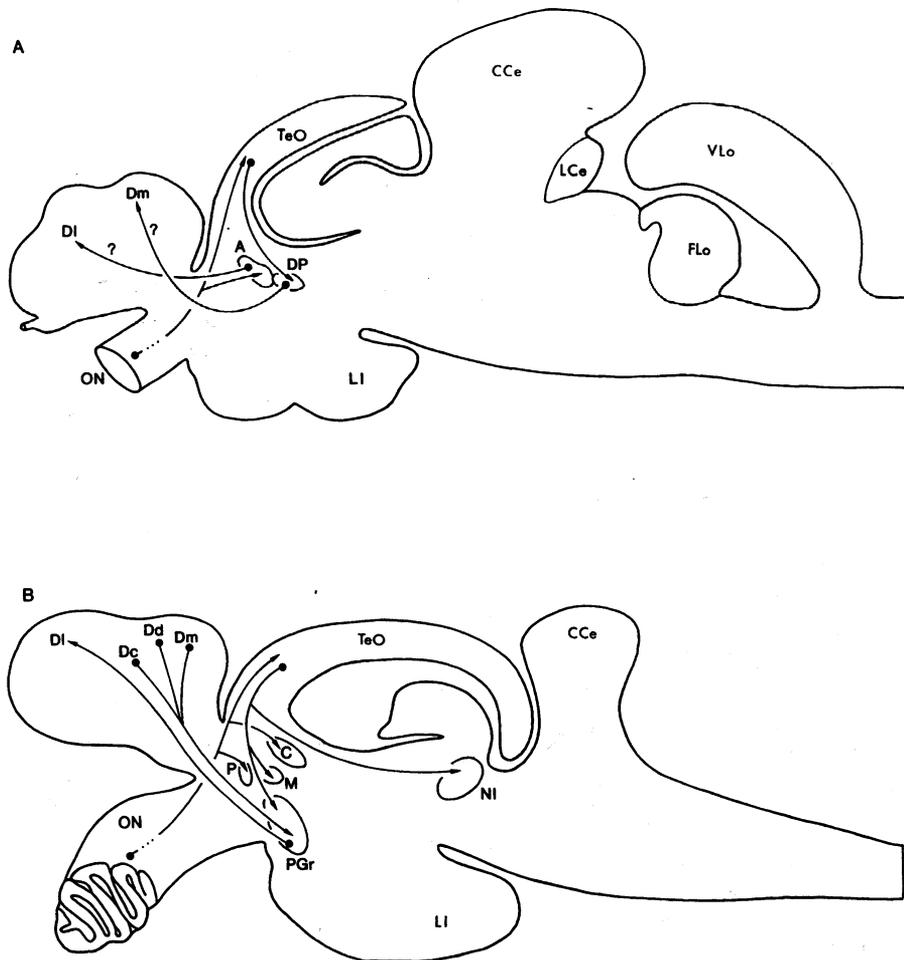
FIGURE 4. Ascending visual pathways in (A) cyprinids[59] and (B) holocentrids.[42,56,97,98,228]

However, independent of the identification of their telencephalic targets, those two ascending visual pathways appear to be much weaker in teleosts in comparison with those of the non-teleost (cladistian; Figure 1B) actinopterygian fish *Polypterus palmas*,[175] suggesting that these pathways may have become secondarily reduced in teleosts.

In some percomorph teleosts (holocentrids: genera *Holocentrus, Myripristis, Adioryx*), a third ascending visual pathway to the telencephalon (Figure 4B) arises in a most rostral part

of the preglomerular area ("nucleus prethalamicus" of other authors (see Reference 188). This rostral preglomerular nucleus receives a strong tectal input[97,98] and projects to the telencephalon (probably the lateral zone of the area dorsalis[54,97,101]). Because of its strong tectal input, the magnocellular superficial pretectal nucleus of cyprinids — although it does not project to the telencephalon — has been misidentified as "nucleus prethalamicus".[96] In cyprinids, most preglomerular nuclei (including the most rostral preglomerular division) project to the telencephalon,[235] but there is no strong tectal input — typical for "nucleus prethalamicus" — to any of those nuclei.[79,130] Since cyprinids appear to lack a tectorecipient "nucleus prethalamicus" within the preglomerular region, this third visual pathway of holocentrids might represent a derived condition for some percomorph teleosts (Figure 1B). However, the osteoglossomorphs *Pantodon buchholzi* and *Gnathonemus petersi* have a rostral preglomerular nucleus which projects to the telencephalon in both species[238,241] and — only in *Pantodon buchholzi* — receives a strong tectal input (M.F. Wullimann, unpublished data). The presence of this visual preglomerulo-telencephalic pathway (so far only described in percomorph holocentrids) in an osteoglossomorph species — the outgroup of all other teleosts (Figure 1B) — sheds new light on its phylogeny. Further data are needed to decide whether this pathway represents a condition shared by all teleosts and is lost at various occasions or, alternatively, originated at least twice independently in osteoglossomorphs and holocentrids.

The pretectum is the most variable visual subsystem in teleosts. Although three major patterns of pretectal organization in different teleosts have been recognized,[234,243] very little is known concerning their functional context. The most consistently observed retinorecipient teleostean pretectal nucleus is the central pretectal nucleus. It likely is the homologue of the lentiform mesencephalic nucleus of other nonmammalian vertebrates, and thus may be functionally closely associated with the accessory optic nuclei in oculomotor reflexes. Single-cell recordings in the central pretectal nucleus demonstrate small receptive fields (average: 8.6°), absence of habituation, and strong directionality in the horizontal plane; the best stimulus is a slowly moving object.[74] Also, little interspecific variation is seen in the retinorecipient dorsal periventricular pretectal nucleus. Its functional context is within respiratory motor activity (see Section II.B.1).

In contrast, the superficial pretectum is highly variable in teleosts, both in the number of nuclei and in their degree of histological differentiation. An elaborate pattern of pretectal organization is present in the most derived group of teleosts, the percomorphs (Figure 1B). There it involves a major visual pathway from the retinorecipient parvocellular superficial pretectal nucleus via the intermediate superficial pretectal nucleus and nucleus glomerulosus to the hypothalamic inferior lobes, which, in turn, has descending projections to the medulla oblongata[209,225,234] (Figure 5B). In addition, this pathway is paralleled by a visual — possibly cholinergic[234,240] — input from the retinorecipient neurons of nucleus corticalis to nucleus glomerulosus.[209] Comparative studies suggest that a similar, slightly less (intermediately) complex, pretectal visual circuitry (Figure 5A) existed at the outset of teleostean evolution.[234,243] The size and degree of differentiation of nuclei and tracts involved in the retinopretecto-hypothalamic pathway is astonishing and represents a unique specialization of teleosts. Electrophysiological evidence suggests a role of this visual subsystem in the detection of moving objects,[207,231] a function generally ascribed to the tectum in other vertebrates. Clearly, more knowledge on the functional context of this conspicuous subsystem is necessary before the visual system of teleosts can be fully evaluated.

In comparison, cyprinids have a distinctly altered pretectal organization and circuitry[188] (Figure 5C). Goldfish and carp have a rather small retinorecipient parvocellular superficial pretectal nucleus and nucleus corticalis is absent. Unfortunately, the (preglomerular) tertiary gustatory nucleus of cyprinids has been misidentified as the (visual) nucleus glomerulosus occasionally (see Section II.A.7). However, cyprinids do have a separate, if small, posterior pretectal nucleus,[234] which represents the homologon of the large posterior pretectal nucleus/nucleus glomerulosus of the other two pretectal patterns (Figure 5A,B). Although it
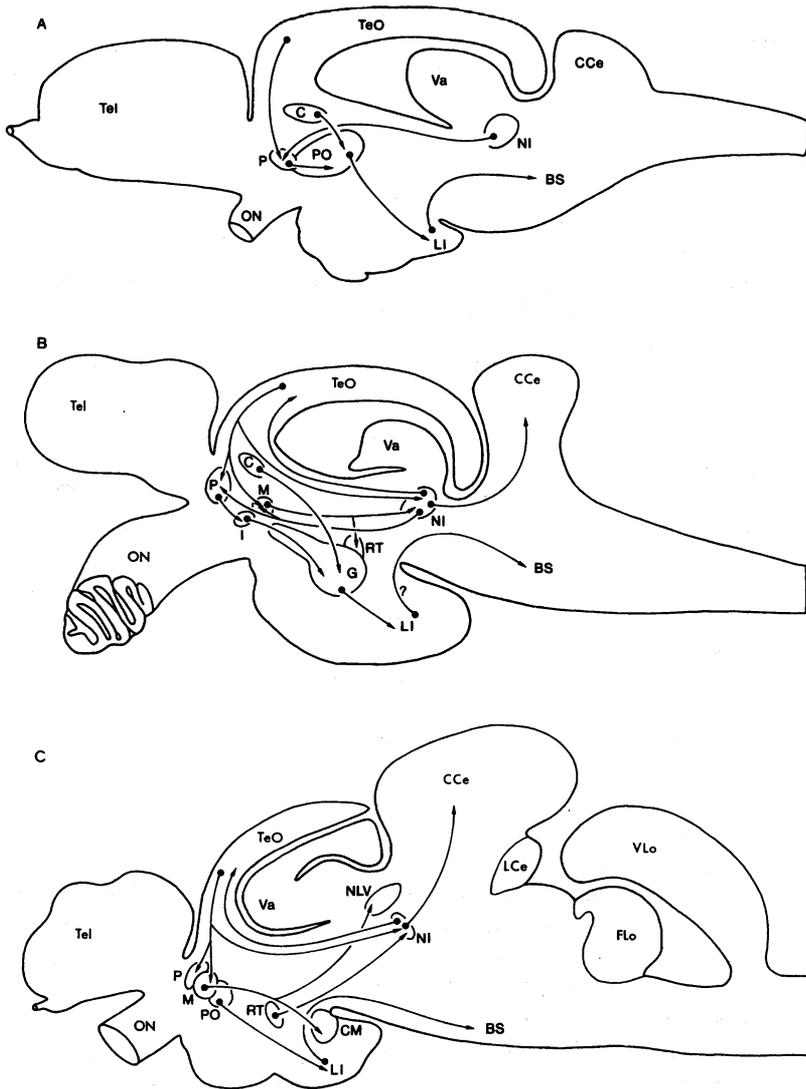
FIGURE 5. Visual circuitry in (A) the plesiomorphic (intermediately complex) pretectal pattern, e.g., *Osteoglossum bicirrhosum*,[243] (B) in the apomorphic (elaborate) pretectal pattern of acanthomorphs,[166,209,225] and (C) in the apomorphic (simple) pretectal pattern, e.g.. cyprinids.[113,185]

is unclear whether the parvocellular superficial pretectal nucleus projects to the posterior pretectal nucleus in the goldfish, efferents of the latter nucleus to the hypothalamic inferior lobes were recently discovered (E. Rink and M.F. Wullimann, unpublished data). These connectional data support the interpretation of a reduced (simple) pattern of pretectal organization in cyprinids. The large tectorecipient magnocellular superficial pretectal nucleus projects to the mammillary body and to nucleus lateralis valvulae in cyprinids[99,185,247] (Figure 5C), while in percomorphs the same-named tectorecipient nucleus projects to nucleus isthmi and to the rostral tegmental nucleus ("lateral thalamic nucleus" of Striedter and Northcutt[225]; Figure 5B). Single-cell recordings in the magnocellular superficial pretectal nucleus of a percomorph species revealed large receptive fields (average 20.2°), absence of directionality, and no habituation, neurons responded both to stationary cues and moving objects.[74] Thus, it appears that the efferents — but not the afferents from the tectum — of the cyprinid magnocellular superficial pretectal nucleus are entirely different from its

percomorph counterpart, and that the visual circuits running via the parvocellular superficial pretectal nucleus are highly reduced in cyprinids.

The dorsal and ventral accessory optic nuclei of teleosts receive retinal input and are involved in optokinetic oculomotor reflexes (see Sections II.B.1 and II.C.1). The retinorecipient (preoptic) suprachiasmatic nucleus may be involved in circadian rhythm generation and control as in other vertebrates. Additional retinal fibers terminate in the preoptic region lying dorsal and caudal to the the suprachiasmatic nucleus.[40,145,186] Interestingly, the suprachiasmatic nucleus — in contrast to the often-lost accessory optic nuclei — is always retained in vertebrates with a secondarily reduced visual system (e.g., in the blind cave fish).

Central nervous efferent projections to the teleostean retina arise at diencephalic and rhombencephalic levels.[188]

3.   Mechanoreception

The term "mechanoreception" is used here exclusively for mechanosensory signals sensed by hair cells in neuromasts of the lateral line system and not for the tactile component of the trigeminal somatosensory system. Mechanosensory information reaches the brain via the lateral line nerves. In most aquatic vertebrate groups, the lateral line nerves encode a second sensory modality, i.e., electroreception (see below). The mechanosensory neuromasts detect the relative movement (acceleration) between water and animal at low frequencies (1 to 200 Hz) and at relatively short distances (1 to 2 body lengths) in various biological contexts such as prey localization, navigation, and schooling behavior.[46]

Lateral line nerves are characterized by embryonic origins (separate placodes), and by adult sensory ganglia, sensory organs (neuromasts), as well as central projection nuclei, which are all different from those of other cranial nerves.[139,181] Lateral line nerves, thus, are cranial nerves in their own right and do not represent the "special somatosensory component" of the facial and vagal nerves. In teleosts, an anterior and a posterior lateral line root enters the brain. With respect to the number of separate ganglia and peripheral innervation patterns, both lateral line roots contain at least two separate nerves and the plesiomorphic number of lateral line nerves in gnathostomes is even higher.[181] The lateral line nerves project to a dorsal medullary area between cerebellum and vagal lobe. This mechanoreceptive area is divided into a medial and a caudal octavolateralis nucleus. Additional lateral line projections always reach the cerebellar granular eminence and, in a few species, corpus and valvula cerebelli.[242]

Second-order projections from these two nuclei ascend in the lateral longitudinal fascicle (Figure 6) and terminate bilaterally, albeit with a stronger contralateral component, in the lateral portion of the torus semicircularis[50,72,117,140] which, in turn, projects to the lateral preglomerular nucleus.[57,140,143,164,165,223] This diencephalic nucleus provides one of the strongest and interspecifically most consistent inputs to the area dorsalis telencephali, though to slightly variable subregions in different species.[164,165,224] For example, in catfishes and in cyprinids, the lateral, medial, and central zones of area dorsalis telencephali all receive input from the lateral preglomerular nucleus, but the dorsal zone only does so in catfishes and not in cyprinids.

There are descending projections within the teleostean mechanosensory system. In most species investigated, the medial and central zones of area dorsalis telencephali project back onto the lateral preglomerular nucleus. However, there are no descending projections from the lateral preglomerular nucleus to the torus semicircularis. The mechanosensory nucleus of the torus semicircularis (nucleus ventrolateralis) projects via a brainstem nucleus, the preeminential nucleus, to the primary sensory medial octavolateralis nucleus.[69,143,223] The preeminential nucleus also receives ascending input from the medial octavolateralis nucleus.

The mechanosensory system — in contrast to the electrosensory system — has efferent neurons in the vicinity of the facial motor nucleus (see Section II.B.1).
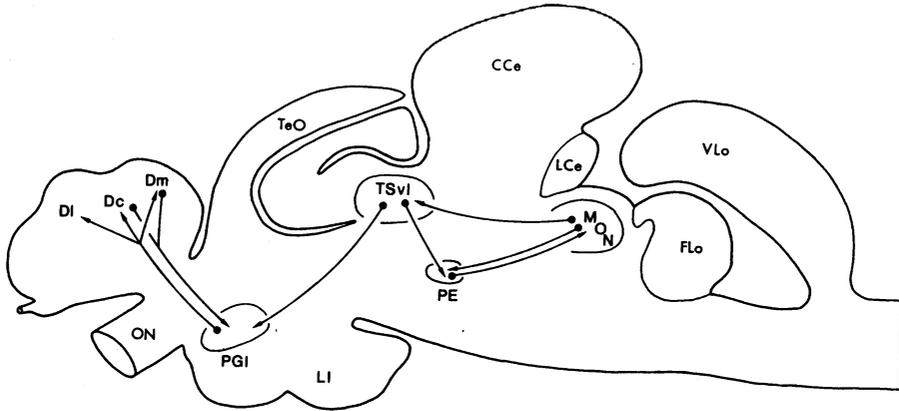
FIGURE 6. Ascending mechanosensory pathways in cyprinids.[143,165,224,235]

4. Electroreception

As all other sensory systems described here, the perception of weak electric fields (electroreception) is a plesiomorphic character of vertebrates (and maybe of all craniates). However, electroreception is lost at the base of the actinopterygian fishes (i.e., in neopterygians; Figure 1B) and is regained at least twice in teleosts.[39] Within the osteoglossomorph notopteroids, the African mormyrids and the African — but not the Asian! — knifefishes (*Xenomystus nigri*) are electrosensitive, a fact that sheds some doubt on the monophyly of notopterids.[34] Secondly, among the ostariophysans, both the gymnotoids (South American knifefishes) and their sistergroup, the siluroids (catfishes[69]) are electroreceptive.[38] Of all teleostean taxa mentioned, only the mormyrids (e.g., *Gnathonemus*) and the gymnotoids (e.g., *Apteronotus, Eigenmannia*) have developed an active electrosensory system. It enables these animals — in addition to passively sensing external electric fields — to actively emit electric signals through a weak electric organ and to perceive these signals with specialized sensory organs in order to perform electrolocation and electrocommunication.[24,38] The degree of parallelism in the electrosensory systems of the distantly related mormyrids (Osteoglossomorpha) and gymnotoids (Ostariophysi; Figure 1B) is striking. Both teleost groups exhibit three types of electroreceptors, the first one is specialized for low-frequency (passive) electroreception (ampullary organs, also present outside the actinopterygians), the other two are dedicated to high-frequency (active) electrolocation and electrocommunication (two types of tuberous organs exclusive for these teleosts). Furthermore, parallel processing of these electrosensory submodalities is maintained in the CNS at least up to the midbrain.[20,43,224,238] However, many differences in the electrosensory systems of mormyrids and gymnotoids are vivid testimony of their having an independent evolutionary origin. Whereas the torus semicircularis is laminated in gymnotoids, it is subdivided into distinct nuclei in mormyrids.[18,44,211] Although an enlargement of the cerebellum is correlated with the electric sense in both groups, different cerebellar parts are hypertrophied in gymnotoids (corpus cerebelli) and mormyrids (valvula cerebelli, Figure 2J).

As in all fishes, teleostean electroreceptors and mechanoreceptors (neuromasts) are innervated by lateral line nerves. Whereas in mormyrids the head is innervated by the anterior and the body trunk by the posterior lateral line nerve root,[17,19] in gymnotoids all electroreceptors (but not the mechanoreceptors) are innervated exclusively by the anterior lateral line nerve root.[45,137] Both teleost groups have an anterior lateral line lobe in the rostral medulla oblongata which receives mechanosensory projections as well as a much larger posterior lobe dedicated to electrosensation. The primary afferents coming from the two types of tuberous organs (electrolocation/electrocommunication) are segregated within the posterior lobe. For

comparative reasons, the mechanosensory anterior lobe will here be referred to as the medial octavolateralis nucleus and the posterior lobe as the electrosensory lateral line lobe (ELL).

Contrary to most other teleosts (see Section II.A.5), in mormyrids both the octaval nerve and the lateral line nerves have projections to the medial octavolateralis nucleus (anterior lobe of Bell[17]) and to the anterior octaval nucleus, but the terminals overlap only slightly within these nuclei.[17] McCormick,[141] therefore, interprets the medial (auditory) part of the medial octavolateralis nucleus in mormyrids as part of the descending octaval nucleus.

The ascending connections of the mechanosensory lateral line system in actinopterygians run from the primary sensory medial octavolateralis nucleus via the torus semicircularis to the lateral preglomerular nucleus which, in turn, projects to the telencephalon. These pathways are well documented in gymnotoids[221,224] and catfishes.[223] Comparable mechanosensory pathways (Figure 7A) were identified in mormyrids.[18,84] The ascending connections involved with electrolocation[22,73,238] resemble the mechanosensory ones in that they too run via the torus semicircularis and one nucleus of the preglomerular region (Figure 7B). Electrocommunication-related pathways run differently in mormyrids. Although they ascend similarly to the torus semicircularis, they are then relayed via several midbrain centers to the valvula cerebelli.[73,83] Interestingly, both the valvula and the corpus cerebelli[73,150,151] are also in receipt of connections originating in several centers of the ascending pathways of mechanosensation and electrolocation (Figure 7B). These inputs to the cerebellum clearly represent a specialization of mormyrids.[238] Unique among all vertebrates is a direct connection of the (electrolocation-related) medial leaf of the valvula[208] to the telencephalon in *Gnathonemus petersi*.[239] Although the extensive inputs to the cerebellum are absent in gymnotoids and catfishes, their respective ascending electrosensory pathways run similarly up to the torus semicircularis, as in mormyrids. From there, they are relayed first via a pretectal nucleus (nucleus electrosensorius) before reaching the preglomerular region, and finally the telencephalon.[111,221,223,224]

Alternatively, Braford and McCormick[35] proposed that the mechanosensory pathway via the ventral preglomerular nucleus of mormyrids (Figure 7A) is purely auditory. They further consider the dorsal preglomerular nucleus associated with electrolocation (Figure 7B) to represent the ventral tegmental nucleus of nonelectrosensitive teleosts where this nucleus projects to the cerebellum[236,237] (Figure 12A,B). However, their hypothesis is not supported by new data, and furthermore offers no explanation for the cerebellar afferents originating in the ventral preglomerular nucleus and torus semicircularis.

In summary, the ascending electroreceptive pathways in mormyrids and gymnotoids are very similar up to the midbrain, but differ drastically from midbrain to telencephalon.

The specialized descending motor pathways controlling the electromotor cells of the spinal cord that innervate the electric organ are superficially similar in gymnotoids and mormyrids. In the latter, the spinal electromotor neurons are innervated by a group of electrotonically coupled neurons in the medulla oblongata (medullary relay nucleus). Their synchronous signal is initiated and controlled by the presynaptic and nearby located integrative neurons of the command nucleus. This command nucleus, in turn, receives its most important excitatory input from the precommand nucleus in the diencephalon.[23,78,149] The command nucleus emits via collaterals a signal that reaches multisynaptically the (primary sensory) ELL.[21,25,149] The latter therefore receives information on the reafference (the self-generated electric signal) in addition to the primary sensory exafference (signals emitted by conspecifics). This collateral circuit filters out all self-generated signals via inhibition in the nucleus of the ELL, which processes primary sensory information stemming from the knollenorgans (electrocommunication). In the large remainder of the ELL concerned with electrolocation, the responses of the primary sensory neurons are affected by this collateral input in a more complex way, reflecting the discrimination of the reafference vs. exafference.[149]
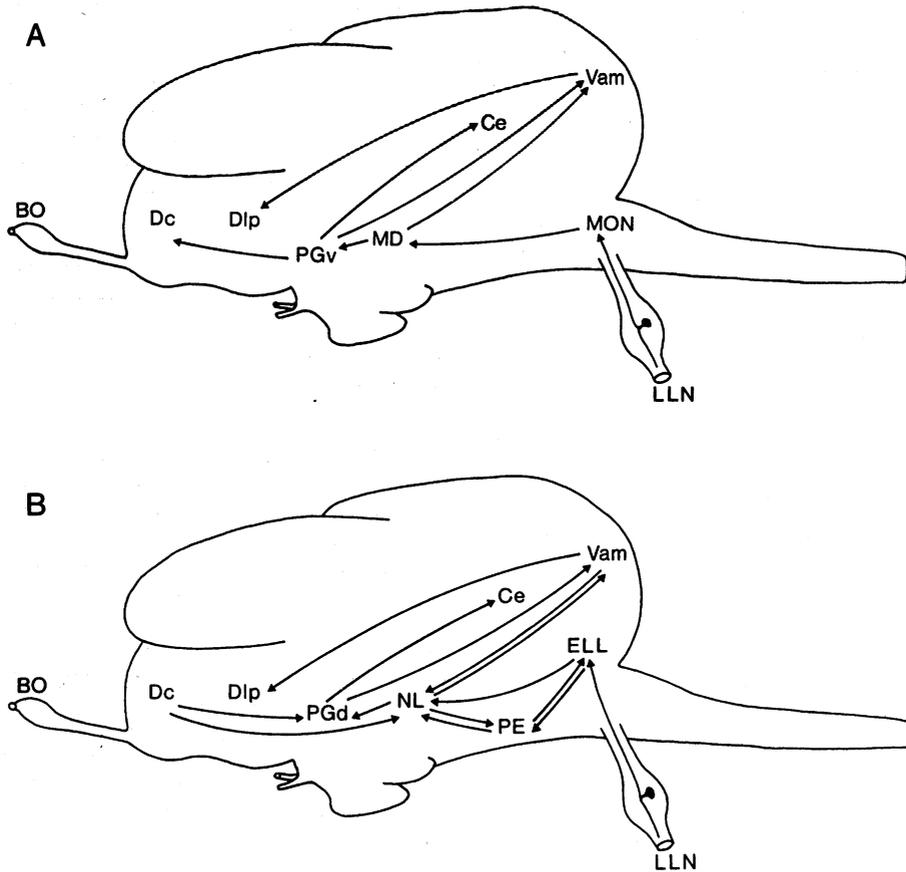
FIGURE 7. Ascending lateral line pathways in mormyrids (see Reference 241). (A) mechanosensory system, (B) electrosensory (electrolocation) system.

Similarly, gymnotoids have a medullary relay nucleus which directly innervates the electromotor spinal neurons and a group of neurons (pacemaker cells) that are presynaptic to the medullary relay nucleus. Both neuronal populations together are called pacemaker nucleus in gymnotoids. Also comparable to mormyrids is a diencephalic nucleus, the prepacemaker nucleus, which — apart from the sublemniscal prepacemaker nucleus — represents the only input to the pacemaker nucleus.[43,77,87,88,110] However, the pacemaker nucleus of gymnotoids does not have collaterals which could serve as a starting point for a multisynaptic network reaching the ELL, as in mormyrids.[77] The central nervous premotor/motor system just described for gymnotoids has been intensely studied in the context of the jamming avoidance response,[86] a behavior that serves the avoidance of sensory interference between self-generated electric signals and those of conspecifics.

5. Audition

The auditory capabilities of many, if not all, teleosts are impressive.[193,229] Auditory signals are perceived for considerably greater distances compared to mechanosensory signals, and the perceived frequency range is up to 3000 Hz. Rather surprising is the fact that synthetic listening (several components of a complex signal are grouped together) and analytic listening (identification of one component of a complex signal) occur in goldfishes,[62] since these behaviors were long thought to be unique to mammals.

The peripheral auditory sensory organs are one or more otolithic end organs of the inner ear. Sensory fibers innervating hair cells of various endorgans of the inner ear form the octaval nerve which encodes vestibular as well as auditory information. In contrast to the older view of a common primary sensory "octavolateralis area" receiving both lateral line and octaval nerve projections, it is now accepted that the primary projections of these nerves are segregated into a dorsal mechanosensory (lateral line) column and a ventral octaval column.[139,141] The octaval nerve projects to five nuclei comprising this octaval column. These are the anterior, magnocellular, descending, tangential, and posterior octaval nuclei. Similar to the lateral line nerves, in all teleosts investigated the octaval nerve (probably vestibular fibers) additionally projects to the cerebellar granular eminence,[242] where the octaval input is spatially segregated from the lateral line input. The corpus and valvula cerebelli generally do not receive primary octaval input. A small zone of overlap between primary lateral line and octaval projections exists in a limited part of the teleostean magnocellular octaval nucleus. Moreover, in the herring *Clupea harengus*,[152] in the eel *Anguilla anguilla*,[153] and in the catfish *Ancistrus* sp.,[28] octaval projections also terminate in part of the (mechanosensory) medial octavolateralis nucleus. The functional significance of these cases of limited mechanosensory-octaval overlap of primary projections is unclear.

Different endorgans in the utriculus, sacculus, and lagena can be specialized for audition in various teleosts.[28,91,193] Correlated with these peripheral auditory specializations, some variation in the primary sensory central nuclei related to audition exists. In the toadfish *Opsanus tau*,[91] the dorsal part of the anterior octaval nucleus, and in cyprinids, additionally, the dorsomedial part of the descending octaval nucleus[57,58,142] have been identified as primary auditory centers. In cyprinids, secondary octaval projections from these two nuclei ascend in the lateral longitudinal fascicle (Figure 8) and terminate bilaterally (stronger contralaterally) in the medial part of the torus semicircularis (central nucleus) and (stronger ipsilaterally) in a secondary octaval population of neurons.[57,143] Interestingly, this secondary octaval population of neurons projects to the central nucleus of the torus semicircularis and may be homologous to the superior olive of mammals. The central nucleus of the torus semicircularis projects to the central posterior thalamic nucleus;[57] the auditory function of the latter is physiologically established.[126] Although it has been demonstrated physiologically that the central and the medial zone of area dorsalis telencephali process auditory information,[58] in cyprinids, direct projections from the central posterior thalamic nucleus to these telencephalic regions have not been documented.[235] The latter may thus receive already higher-order auditory input from within the telencephalon. However, the central posterior thalamic nucleus undoubtedly projects to the telencephalon in some teleost species,[223,238] but its main telencephalic target may be within the area ventralis.[223] Additional auditory pathways that ascend
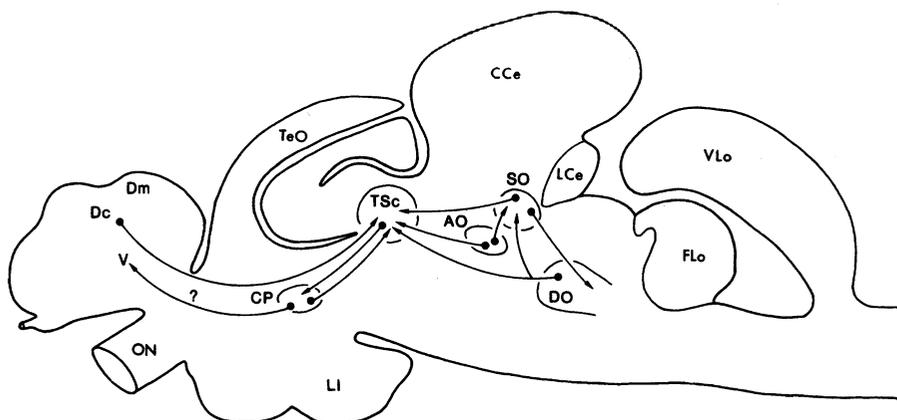

FIGURE 8. Ascending auditory pathways in cyprinids.[57,58,143]

from the torus semicircularis via the diencephalon to the telencephalon have evolved as specializations of the acoustic system in other teleosts, e.g., via the ventromedial thalamic nucleus in *Sebastiscus marmoratus*[164] or via the tuberal hypothalamus in catfishes.[223]

The descending projections in the cyprinid auditory system include a projection from the secondary octaval population back to the descending octaval nucleus as well as a projection from the central posterior thalamic nucleus and from the central zone of area dorsalis telencephali to the auditory torus semicircularis.[57,143] Similar to the mechanosensory system, the auditory system has efferent neurons in the vicinity of the facial motor nucleus (see Section II.B.1).

6.   Vestibular Sense

The peripheral receptor cells that mediate the sense of balance are found in the inner ear semicircular canal and otolithic endorgans. Some of these sensory organs have a dual function in teleosts, since they are also involved in hearing.[193] Vestibular signals reach the nuclei of the octaval column from the peripheral receptor cells by way of the eighth cranial nerve. Three of the five primary octaval nuclei described above, i.e., the magnocellular, tangential, and posterior octaval nuclei, likely are exclusively vestibular. However, parts of the anterior and descending octaval nuclei also receive vestibular information. All of the primary vestibular areas project to the spinal cord (see Section II.B.2) and do not appear to have ascending projections. This is in contrast to the auditory areas of the anterior and descending octaval nuclei which have only ascending projections (see Section II.A.5). Projections of primary vestibular nuclei to motor nuclei of extraocular muscles are discussed below (see Section II.B.1).

7.   Gustation

The gustatory system of fishes can be differentiated from the olfactory system primarily based on its peripheral and central anatomy. Functionally, the two systems are harder to distinguish. Unlike in land vertebrates, the chemical cues for both systems are carried in an aqueous medium. Also, the gustatory system of fishes is active at long distance as is the olfactory system. Furthermore, there is overlap between the two systems with respect to chemicals perceived, i.e., for amino acids. However, the gustatory system of a particular fish — in strong contrast to the olfactory system — is most sensitive to a highly species-specific composition of amino acids.[82]

Three cranial nerves, the facial, the glossopharyngeal, and the vagal nerves, contact the multicellular peripheral sensory organs (taste buds) that are specialized to perceive environmental gustatory cues. These three cranial nerves project to the medullary gustatory (special viscerosensory) column. In fishes with a well-developed taste system, this column consists of separate primary gustatory centers for each nerve, i.e., facial, glossopharyngeal (= intermediate), and vagal lobes.[105,107,127,158,196] Projections of the glossopharyngeal nerve also reach part of the vagal lobe. The vagal nerve further projects to the medial funicular nucleus and to the commissural nucleus of Cajal (which represents the general viscerosensory nucleus).

While taste buds on the head and body trunk (extraoral system) are innervated by the facial nerve, those in the oropharynx and on the gill arches (intraoral system) are innervated by the glossopharyngeal and vagal nerves. Hypertrophy of the gustatory system has occurred in several groups of teleosts independently, the two best investigated groups being the siluroids (catfishes) and the cyprinids (carp, goldfish). The former have a relatively better developed extraoral system, whereas the cyprinids have emphasized the intraoral system. This difference is also reflected in the central nervous representation of the different gustatory components in the two teleost groups. The facial lobe is larger and more complex in siluroids[85] and the vagal lobe is larger and more complex in cyprinids.[156] Most siluroids have extensive barbels densely populated with taste buds and they use this extraoral system for food search and

sorting, whereas their intraoral taste system is used for selective food ingestion.[4] Although this functional division generally also applies to cyprinids, the latter rely much more on their intraoral gustatory system, especially the palatal organ located in the oropharyngeal roof, for sorting of food.[216] The entire oropharyngeal cavity, including palatal organ and gill arches, is topographically represented in the vagal lobe (viscerotopy), with sensory and motor components of the peripheral oropharynx in radial (laminar) register.[155] This arrangement allows for point to point reflex arches involving oropharynx and vagal lobes.

Functional interactions between gustatory and tactile systems exist at several levels in cyprinids and siluroids: (1) primary sensory trigeminal and facial projections originating in the mandibular periphery overlap in a limited ventral area of the facial lobe,[116,196,197] and similarly, the medial funicular nucleus of cyprinids receives primary projections from the trigeminal as well as the vagal nerves;[158,197] (2) secondary gustatory projections from the facial — but not from the vagal — lobe reach the medial funicular nucleus in siluroids and cyprinids;[64,158] and (3) apart from these central interactions of the gustatory and somatosensory systems, the teleostean vagal and facial fibers themselves encode tactile stimuli.[106,114,115,138]

A common pattern of ascending gustatory connections is shared by all teleosts and can be concluded to represent the ancestral pattern for teleosts. The primary gustatory nuclei project via the secondary gustatory tract to a secondary gustatory nucleus in the isthmus which, in turn, projects to the hypothalamic inferior lobes and to a tertiary gustatory nucleus within the medial preglomerular area.[64,106,118,119,156,158,159,232] As pointed out by Braford and Northcutt,[36] this preglomerular tertiary gustatory nucleus has been misidentified as "nucleus glomerulosus" in cyprinids. The latter term definitely should be restricted to the visually related nucleus seen in more derived teleosts (see Section II.A.2). The lateral torus is also a tertiary gustatory center in cyprinids and percomorphs[232] but not in siluroids.

Both siluroids and cyprinids elaborate on this basic gustatory circuitry in slightly different ways (Figure 9). Facial, glossopharyngeal and vagal lobes, as well as the secondary gustatory nucleus, are greatly enlarged and histologically more complex in these fish compared to species which show the plesiomorphic pattern. However, the emphasis is on the facial lobe in siluroids and on the vagal lobe in cyprinids. While cyprinids have a single preglomerular tertiary gustatory nucleus, siluroids show two such preglomerular centers, the nucleus of the lateral thalamus, which is homologous to the cyprinid tertiary gustatory nucleus, and a more posteriorly located nucleus lobobulbaris.[118,119,158,159] Different tertiary gustatory centers, the inferior lobe in cyprinids and the lobobulbar nucleus in siluroids, develop extensive descending connections to the (primary gustatory) facial and vagal lobes.[156,159] In cyprinids, such descending connections also originate in the posterior thalamic nucleus. Thus, although the latter nucleus does not receive tertiary gustatory input in cyprinids, it may be homologous to the lobobulbar nucleus of siluroids. Furthermore, the nucleus of the lateral thalamus in siluroids (but not the preglomerular tertiary gustatory nucleus in cyprinids) projects back to the secondary gustatory nucleus.

Gustatory information does not appear to ascend directly from the diencephalic level to the telencephalon in all teleosts. In cyprinids, neither the preglomerular tertiary gustatory nucleus, the lateral torus, nor the inferior lobe project to the telencephalon, but the posterior thalamic nucleus does so.[235] It was recently discovered that the posterior thalamic nucleus of the goldfish is reciprocally connected with at least two tertiary gustatory centers (inferior lobe/lateral torus; E. Rink and M.F. Wullimann, unpublished data). Thus, the posterior thalamic nucleus clearly is functionally linked to the central nervous gustatory system in the goldfish and likely represents the diencephalic gustatory projection nucleus to the telencephalon in cyprinids. In siluroids, direct projections from tertiary gustatory centers to the telencephalon exist. The nucleus lobobulbaris projects to the medial zone and central zones of the dorsal telencephalic area and the central nucleus of the inferior lobe projects to the central
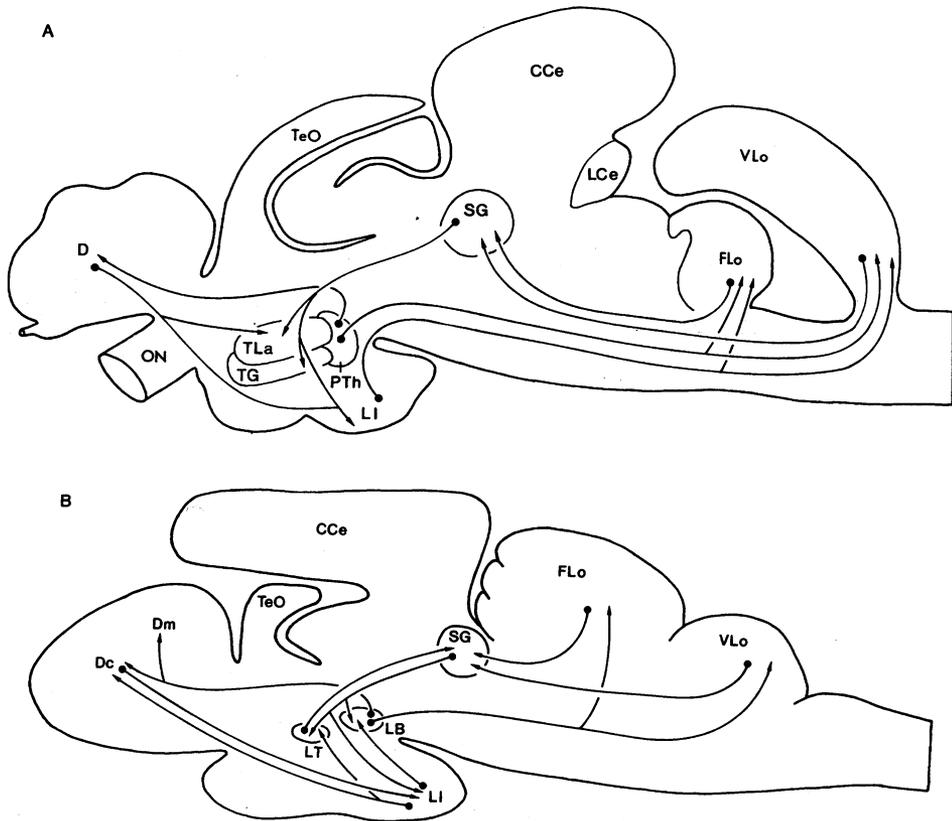
FIGURE 9. Ascending gustatory pathways in (A) cyprinids[156,158,159] and (B) catfishes.[64,108,118,119]

zone of the dorsal telencephalic area.[108,118,119] Also, connections between tertiary gustatory nuclei do exist. The central nucleus of the inferior lobe projects to the lobobulbar nucleus and to the nucleus of the lateral thalamus.[108,118,119] Thus, whereas the connections of the nucleus lobobulbaris seem to support its homology with the cyprinid posterior thalamic nucleus, the ascending telencephalic connections of the inferior lobe appear to be an apomorphic condition for siluroids.

In summary, different elaborations of ascending and descending connections in the gustatory system characterize cyprinids and siluroids in comparison to the ancestral teleostean condition, and these differences likely represent the neural basis for behavioral differences in food handling.

8. General Visceral Sense

In addition to the special viscerosensory modality (gustation), the teleostean vagal nerve also encodes general viscerosensory stimuli from the viscera to the CNS, notably to the nucleus commissuralis of Cajal. In the goldfish, this nucleus has lateral and medial subdivisions, the lateral one receiving general viscerosensory input from the posterior pharynx (region of the chewing organ immediately rostral to the esophagus) and the medial one from the gastrointestinal tract.[157] Also the vagal motor neurons are segregated into lateral and medial populations, the lateral one innervates the posterior pharynx and the medial ones innervate the gastrointestinal tract. A set of even more medially lying motoneurons innervate the heart. Similar to the situation in the vagal lobe, reflex arches exist for the posterior pharynx

and the viscera via the related sensory and motor nuclei.[75] The motoneurons innervating the heart and the medial visceromotor subnucleus subserving the gastrointestinal tract are the homologue of the mammalian (parasympathetic) nucleus dorsalis nervi vagi. The lateral visceromotor subnucleus innervating the posterior pharynx plus the motor layer in the vagal lobe innervating the oropharynx and gill arches are together homologous to the mammalian nucleus ambiguus. The nucleus commissuralis of Cajal together with the sensory layers of the vagal lobe are homologous to the mammalian nucleus solitarius.

Secondary general viscerosensory projections in siluroids and cyprinids ascend in parallel with the secondary gustatory projections and terminate in a discrete (calcitonin gene-related peptide-rich) area ventrally adjacent to the secondary gustatory nucleus.[70] Tertiary general visceral projections are not known in teleosts.

9.   Somatosensation

In the sockeye salmon *Oncorhynchus nerka*, spinal axons ascend in the lateral funiculus and reach cranial nerve motor nuclei, vagal lobe, reticular formation, cerebellum, and torus semicircularis. Ascending spinal fibers running in the dorsal funiculus only reach up to the junctional region (obex) between spinal cord and brainstem.[192] This presence of two separate ascending systems resembles the anterolateral and dorsolateral ascending spinal systems, respectively, in mammals. In the scorpaenid *Sebastiscus marmoratus*,[102,161] ascending projections originating in the spinal dorsal horn at the level of the obex reach the thalamus (ventrolateral, ventromedial, and central posterior thalamic nuclei) in addition to most targets reported for the salmon (Figure 10B). The neurons that project to these thalamic targets are located lateral to the vagal lobe and in the most rostral dorsal horn.[102] Consistent with these data, a lateral cuneate nucleus was found in the green sunfish *Lepomis cyanellus*[236] to project to the cerebellum (Figures 10B and 12A). In addition, in the sea robin *Prionotus carolinus*[67] ascending projections were reported from the caudal medulla oblongata to the preglomerular area.

Thus, teleosts appear to have a relay center at the spinal cord-brainstem junction for ascending somatosensory fibers similar to the dorsal column cuneate and gracile nuclei in mammals, in addition to directly ascending spinal projections that are not relayed at this level. In the zebrafish *Danio rerio*, ascending spinal projections (Figure 10A) originating caudal to the level of the first dorsal root appear similar to those described in the salmon, and additionally reach ventral and dorsal thalamus, optic tectum, and most surprisingly, the dorsal nucleus of area ventralis telencephali.[15] This indicates that at least some ascending spinal projections reach the thalamus without being relayed at the spinal cord-brainstem junction. Spinothalamic projections have also been demonstrated in amphibians.[160] Thus, spinothalamic projections may be generally present in anamniotes as well as in amniotes.

Complementary to the ascending somatosensory system which subserves the body trunk periphery, the sensory component of the trigeminal nerve is concerned with somatosensation in the head. These sensory trigeminal projections have been investigated in the carp and the goldfish.[127,197] After entering the rostral medulla oblongata, the sensory root of the trigeminal nerve divides into a rostral bundle and a descending trigeminal root. Whereas the former terminates in the isthmic primary sensory trigeminal nucleus, the descending root provides somatosensory input to the nucleus of the descending trigeminal root and further caudally to the medial funicular nucleus. The (sensory) mesencephalic nucleus of the trigeminal nerve will be discussed later (see Section II.B.1).

The thalamic region indicated above to receive input from the body trunk periphery through direct and indirect spinal ascending somatosensory fibers in *Sebastiscus marmoratus* also gets converging input from the head periphery via the contralateral isthmic primary sensory trigeminal nucleus and the nucleus of the descending trigeminal root (Figure 10B). This somatosensory thalamic region in *Sebastiscus marmoratus*, in turn, appears to project
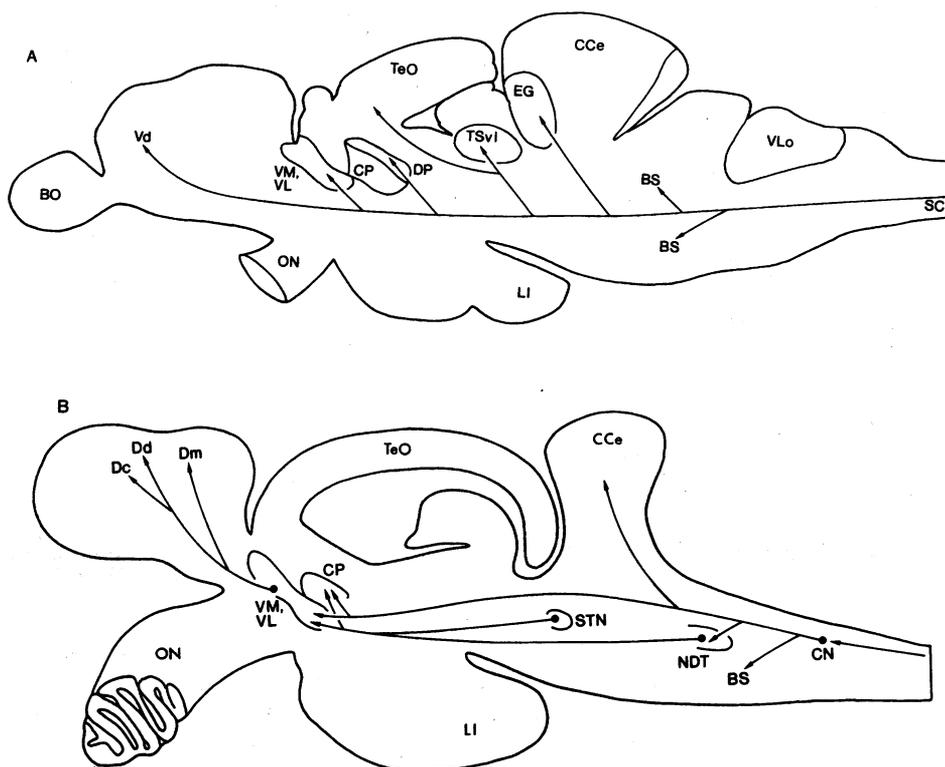
FIGURE 10. (A) Directly ascending somatosensory pathways in the zebrafish *Danio rerio*.[15] (B) Indirectly ascending somatosensory pathways in *Sebastiscus marmoratus*.[102,161]

to the dorsal telencephalic area[102] (central, dorsal, and medial zones), although this was not reported in an earlier extensive study in the same species.[163] However, the ventral thalamus also projects to the caudal part of the medial zone of area dorsalis telencephali in the goldfish,[190] but not to the more rostral portions of the dorsal telencephalic area.[235] Thus, the entire somatosensory body surface appears to be represented in a limited part of the thalamus in teleosts, and this information is relayed from here further on to the telencephalon.

B. MOTOR AND PREMOTOR SYSTEMS

1. Motor Nuclei of Cranial Nerves

In cyprinids, the motoneurons of the oculomotor nerve innervate four of the six extraocular eye muscles (rectus superior, inferior and internus (= medialis), and obliquus inferior), the trochlear motor nucleus innervates the obliquus superior, and the abducens motor nucleus innervates the rectus externus (= lateralis).[76,133] In cyprinids, the abducens motor nucleus consists of small rostral and caudal subnuclei. In the goldfish, the caudal — but not the rostral — subnucleus receives a reticular formation input which may be related to fast eye movements, in contrast to slow eye movements effected by the rostral subnucleus.[2] Also, the oculomotor nucleus receives input from reticular formation neurons[226] and the general functional context of these reticular projections is eye-body motor coordination. As part of the vestibulo-ocular reflex circuitry, the ipsilateral anterior and the contralateral tangential and descending octaval nuclei project to abducens and oculomotor nuclei.[2,226] Neurons in both parts of the abducens motor nucleus project to the contralateral oculomotor nucleus, a projection likely involved in horizontal conjugate eye movements performed simultaneously

by the lateral rectus of one eye and the medial rectus of the other eye. In cyprinids, connections from the primary visual dorsal accessory optic nucleus to the oculomotor nucleus are absent.[226] However, such projections are present in more visually guided teleosts,[71,227] and presumably are involved in the optokinetic ocular reflex (nystagmus).

The trigeminal and facial motor nuclei are involved in a variety of behaviors, from feeding and respiration to aggression, sexuality, and brood care. Here, the motor control of the rhythmic generation of water flow during respiration is considered in order to exemplify the neuronal circuitry of these motor nuclei. In cyprinids, the rostral portions of the trigeminal and facial motor nuclei innervate those muscles of the mandibular and hyomandibular arch that are active during the contraction of the buccal and opercular cavities, while the caudal portions of those motor nuclei innervate the antagonistic muscles performing the expansion of the respiratory cavities.[128,220] Trigeminal and facial motor nuclei are functionally closely linked with regard to respiratory coordination, since they extend dendrites on the ipsilateral side reciprocally and towards their contralateral counterpart. Also, facial and trigeminal motor nuclei receive terminals bilaterally from respiratory-active reticular formation neurons.[134] The reticular formation itself has reciprocal connections with the dorsal periventricular pretectal nucleus and with neurons near the oculomotor nucleus, both of which show rhythmic activity correlated with respiratory movements.[6,103] Whereas electric stimulation of said neurons in the oculomotor region leads to respiratory movements,[103] visual signals and respiratory movements modify the rhythmic activity of the dorsal periventricular pretectal nucleus.[6]

The trigeminal and facial motor nuclei receive input from primary sensory trigeminal nuclei **and** from neurons in the ventral facial lobe, allowing for integrated reflexes towards tactile and gustatory cues. In mammals, the mesencephalic nucleus of the trigeminal nerve contains proprioceptive neurons for the masticatory muscles, i.e., the central fibers of these neurons synapse on motor trigeminal neurons (monosynaptic masticatory reflex). This is different in cyprinids, where proprioceptive neurons for head muscles involved in feeding and respiration (and in oculomotor movements) are mostly located in the peripheral trigeminal and facial nerve ganglia.[129] However, some primary sensory neurons involved in proprioception may additionally be present within the CNS, adjacent to the trigeminal and facial motor nucleus, and if so they would represent the functional equivalent of the mammalian mesencephalic trigeminal nucleus.[129] In every case, the centrally located sensory neurons of the cyprinid mesencephalic trigeminal nucleus appear to be concerned with perioral (exteroceptive) information instead of being proprioceptive.[129]

While the lateral line mechanosensory and octaval systems do not have motor nuclei that innervate muscles, they do have efferent neurons which innervate their peripheral sense organs. All teleosts have one efferent nucleus which lies in the midline of the rhombencephalon at the level of the facial motor nucleus and innervates both mechanosensory neuromasts and inner ear endorgans.[203,204] The goldfish has two efferent neuronal populations in that region and a third one in the diencephalic periventricular area of the posterior tuberculum.[198,248] Because of their intricate anatomical and functional relationship with the gustatory and general viscerosensory systems, the motor nuclei of the glossopharyngeal and vagal nerves have already been treated there.

2.   Descending Spinal Projections

Descending spinal projections were investigated in the sockeye salmon *Oncorhynchus nerka*,[191] in the goldfish,[194] and in the zebrafish *Danio rerio*.[15] In all three species, the descending axons course in the bulbospinal tract, the medial longitudinal fascicle, and the vestibulo-spinal tract, and originate in the Mauthner cell, in all three parts of the reticular formation, in the nucleus of the medial longitudinal fascicle, in the nucleus ruber, and in some of the octaval nuclei. Interestingly, only those octaval nuclei related to vestibular input (magnocellular, tangential, anterior, and the ventrolateral part of descending octaval

nucleus[15,142]) descend to the spinal cord, while the acoustically related dorsomedial part of the descending octaval nucleus does not. In cyprinids (zebrafish, goldfish) the preoptic region, the nucleus of the lateral lemnniscus, and the inferior raphe project, in addition, to the spinal cord (Figure 11). Furthermore, only in the goldfish, a strong spinal projection originates in the facial lobe (associated with the extraoral gustatory system), while only in the zebrafish an additional spinal projection descends from the (mechanosensory) medial octavolateralis nucleus. The functional significance of such interspecific differences in spinal projections between relatively closely related species likely is due to the involvement of different sensory systems in the control of flight reaction.
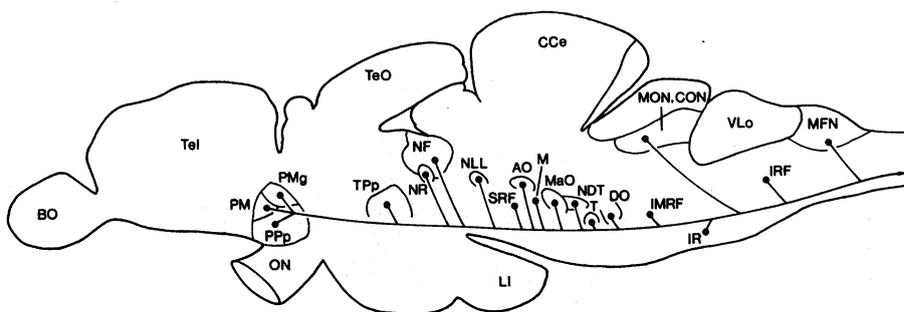

FIGURE 11. Descending spinal pathways in the zebrafish, *Danio rerio*.[15]

Descending spinal projections of teleosts with an active electrosensory system[16,92] — with the exception of some specializations discussed above — are generally similar to those of nonelectrosensitive teleost species.

3. Reticular Formation

The reticular formation constitutes a most complex neuronal network extending throughout the medulla oblongata and into the tegmentum. The rhombencephalic reticular formation may be divided into three longitudinal columns, i.e., a medial one, a lateral one, and a (median) midline column.[173]

The medial column includes a superior, an intermediate, and an inferior nucleus of the reticular formation (for the sake of simplicity termed here the superior, intermediate, and inferior reticular formation) and this column has reciprocal connections with the tectum[33,79,80,130] as well as with the cerebellum;[68,236] medial reticular formation neurons also project to the spinal cord.[122,191,194]

Immediately caudal to the interpeduncular nucleus, reticular formation neurons of the midline column (the serotoninergic superior raphe) project to the telencephalon.[163,235] The inferior raphe nucleus, however, projects to the cerebellum[236] and to the spinal cord.[15] A distinct nucleus of the lateral column is the cerebellar-projecting nucleus reticularis lateralis.[236]

Some additional medullary structures may be considered part of the rhombencephalic reticular formation, such as the Mauthner cell[123] or the locus coeruleus. As in all vertebrates, the latter includes noradrenergic neurons projecting to most brain areas, including the telencephalon.[135,136] The superior reticular formation extends into the tegmentum. Some distinct tegmental nuclei may be considered part of the reticular formation, such as the cerebellar-projecting perilemniscal nucleus and the spinal-projecting nucleus of the lateral lemniscus, as well as the nucleus ruber, which projects to the spinal cord[194] and receives contralateral cerebellar input[236] in cyprinids.

The neuronal network just outlined constitutes the structural basis for the roles of the reticular formation in premotor functions as well as in functions of the ascending (noradrenergic, serotoninergic) activation systems (see Section II.C.3).

C. INTEGRATIVE CENTERS

1. Cerebellum

The teleostean cerebellum includes three parts: the vestibulolateralis lobe (comprising eminentia granularis and caudal lobe), the corpus cerebelli, and the valvula cerebelli. Whereas the teleostean corpus cerebelli lies on top of the rostral rhombencephalon as in all vertebrates, the valvula extends into the tectal ventricle. However, its histology (presence of granular and molecular layers, with an intermediate ganglionic layer consisting of Purkinje cells and eurydendroid cells) and its structural continuity with the rostral rhombencephalon, leave no doubt about it being part of the cerebellum.

The teleostean vestibulolateral lobe is likely to be homologous to the vestibulocerebellum present in all vertebrates (e.g., auricles in many nonteleost fishes, Figure 2), since it receives primary octaval (presumably vestibular) as well as lateral line projections. The inputs to the teleostean corpus cerebelli (Figure 12A) also are largely comparable to those of other vertebrates.[65,236] There is a climbing fiber input from a single source, the inferior olive, as well as various additional, mossy fiber-like inputs originating in the spinal cord, in sensory medullary nuclei, in premotor centers (reticular formation, lateral reticular nucleus), and in the locus coeruleus. Visual input to the corpus cerebelli comes from the pretectum, the nucleus isthmi, and the accessory optic system. However, inputs to the corpus cerebelli from nucleus lateralis valvulae, and from two telencephalorecipient nuclei, the dorsal tegmental nucleus, and from the nucleus paracommissuralis, appear to be apomorphic for teleosts.[100,235]

The valvula cerebelli (Figure 12B) also receives input from the inferior olive and the locus coeruleus, and weaker inputs come from the nucleus lateralis valvulae, the dorsal tegmental nucleus, and from nucleus isthmi, but not from the remaining rhombencephalic nuclei that project strongly to the corpus cerebelli. Thus, a compartmentalization of inputs to corpus and valvula does exist.[236,237] Furthermore, inputs to the valvula differ between species. In the goldfish, the strongest projections to the valvula originate in the isthmic primary sensory trigeminal nucleus, the eminentia granularis and the preeminential nucleus.[237] In mormyrids, the strongest inputs to the valvula come from the preglomerular region and from the torus semicircularis (see Section II.A.4). These structures do not project to the cerebellum in other teleosts species and likely represent specializations of the electrosensory system.[73,238] These interspecific differences of inputs to the valvula cerebelli document its higher plasticity for sensory inputs compared to the corpus. The data discussed support the notion that the corpus is a plesiomorphic part of the cerebellum common to all vertebrates, while the valvula represents an evolutionary new part of the cerebellum representing a synapomorphy of actinopterygians.[171,237]

The efferent cerebellar connections in teleosts (Figure 12C) arise from eurydendroid cells located in the same ganglionic layer as the Purkinje cells from which eurydendroid cells, in turn, receive input.[66,68,148,162,236] Thus, unlike in cartilaginous fishes and tetrapods, there are no deep (efferent) cerebellar nuclei in teleosts. The predominantly contralateral output of the teleostean cerebellar corpus formed by the eurydendroid cells reaches the ventral thalamus and parts of the pretectum, as well as motor and premotor centers such as the oculomotor nucleus, the nucleus ruber, the nucleus of the medial longitudinal fascicle, and the reticular formation.

The cytoarchitectonic properties of the teleostean cerebellar cortex and its input-output characteristics are so similar to other vertebrates that it probably subserves functions in motor learning and coordination as well. A well-investigated example is the role of the lateral
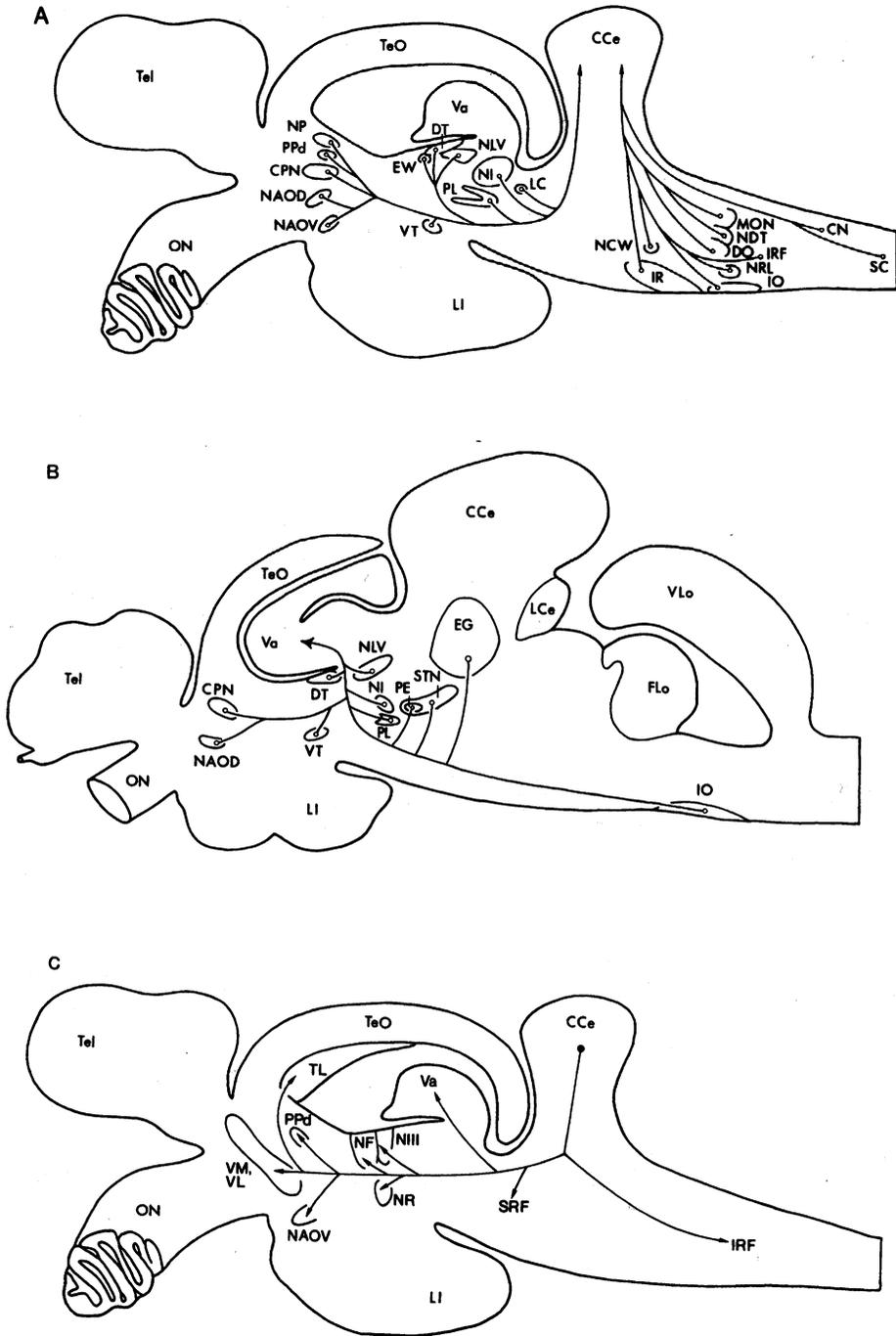
FIGURE 12. Afferent (A,B) and efferent (C) pathways of the cerebellum. (A) Afferents to the corpus cerebelli in the green sunfish *Lepomis cyanellus*. (B) Afferents to the valvula cerebelli in the goldfish *Carassius auratus*. (C) Efferents of the corpus cerebelli in *Lepomis cyanellus*.[236] (Diagram (A) from Wullimann, M. F. and Northcutt, R. G., *Brain Behav. Evol.*, 32, 293, 1988. Copyright Karger, Basel. Diagram (B) from Wullimann, M. F. and Northcutt, R. G., *J. Comp. Neurol.*, 289, 554, 1989. Copyright John Wiley & Sons. With permission.)

division of the valvula cerebelli in the dorsal light response of cyprinids.[154,245,246] However, the size of the valvula and extensive cerebellar representation of sensory systems in at least some teleost species[121,148] raises the question whether additional cerebellar functions in teleosts should be anticipated. Interestingly, a discussion on possible new roles of the mammalian cerebellum (e.g., in cognition) has emerged recently.[124]

2. Tectum Opticum

The teleostean optic tectum is a cortex displaying up to 15 laminae of neurons and neuropil which receive multimodal input from various sources[146,147,177,178] (Figure 13). These include the retina as well as additional visual centers[147,188] such as the dorsal and ventral thalamus, the pretectum, and the nucleus isthmi, but also nonvisual sources such as the torus semicircularis[80,130,177] or the telencephalon (central zone of area dorsalis[1,95]). The ventrolateral nucleus of the torus semicircularis probably is the source of lateral line information to the tectum. In gymnotoids,[13,44] and in mormyrids[238] also electrosensory information reaches the tectum via the torus semicircularis. The input from nucleus isthmi to the tectum is part of a positive feedback system, likely in the context of alerting the tectum to significant visual events.[112,113,189] The torus longitudinalis is a paired, longitudinal eminence of granular cells located in the tectal ventricle, immediately ventral to the midline of the tectum. The longitudinal torus only occurs in ray-finned fishes and many of its neurons project to the most superficial (marginal) tectal layer. The marginal tectal layer of teleosts, therefore, does not consist of retinal terminals as in other vertebrates.[233] The connectivity of the torus longitudinalis reveals that it is part of a multisynaptic pathway descending from the telencephalon to the brainstem.[241]
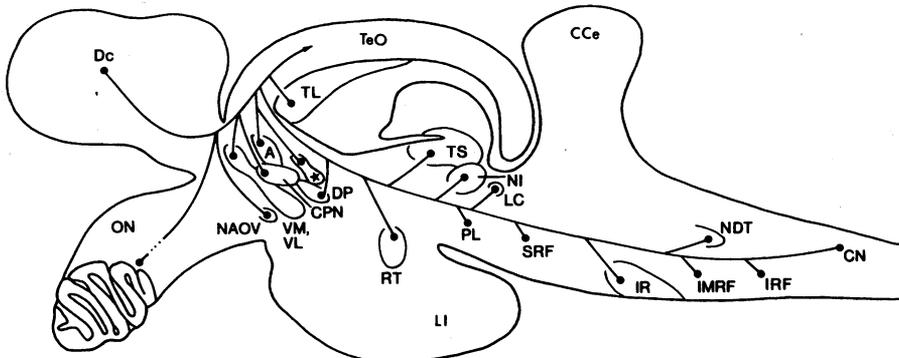

FIGURE 13. Afferent pathways of the optic tectum in the green sunfish *Lepomis cyanellus*. Asterisk: dorsal periventricular pretectal nucleus.[177]

Descending tectal efferents in teleosts reach the ipsilateral nucleus isthmi, a perilemniscal nucleus, the torus semicircularis, and bilaterally, the reticular formation.[56,79,130,217] Ascending tectal projections (mostly ipsilateral) were reported[56,79,130,217] to the longitudinal torus, to the pretectum (e.g., magnocellular superficial pretectal nucleus), to the dorsal and ventral thalamus, to the accessory optic system, and to the preglomerular region ("nucleus prethalamicus", see Section II.A.2). The most detailed description of tectal projections onto thalamus and pretectum exists for the catfish *Ictalurus punctatus*, where tectal terminals were found in the ventral thalamus, in the dorsal posterior thalamic nucleus, in the periventricular nucleus of the posterior tuberculum, in the dorsal and ventral accessory optic nuclei, and in the dorsal periventricular and central pretectal nuclei.[222] Since *Ictalurus punctatus* lacks both parvocellular and magnocellular superficial pretectal nuclei, the tectal projections to those nuclei typical for other teleosts are absent in this species.

All tectal inputs are radially segregated into various tangential bands of terminals; these bands need not be identical with tectal layers. The very numerous (ten times more than retinal axons) periventricular tectal neurons (mostly type XIV of Meek[147]) have a long dendritic arbor which spans radially the whole extent of the tectum, has a variable morphology, and makes pre- and postsynaptic contacts in visual and other layers. While such neurons may perform feature analysis of information gained from various visual and nonvisual sources, their exact function remains elusive in teleosts. The output of some type XIV neurons is to other visually related nuclei (pretectum, thalamus, nucleus isthmi[147]), but most of them are local interneurons. Comparable tectal interneurons with dendritic arborizations in visual layers in amphibians are **not** recipient of direct retinal projections, but they receive nonretinal visual and nonvisual information and have a modulatory role in the analysis of shape and movement (G. Roth, U. Dicke, and W. Grunwald, unpublished data).

Other tectal neurons (types I–XIII) in more peripheral layers are less numerous (10 to 100 times less than retinal axons) and they have regular dendritic arbors and synaptic densities.[147] This suggests that they may integrate different multimodal information aspects. The efferent axons of half of those 13 types of tectal neurons (types III,IV,V,VI,X,XII,XIII) reach premotor centers (reticular formation) and the torus semicircularis. Thus, in cyprinids it appears that periventricular tectal neurons may predominantly have ascending, and more peripheral tectal neurons may have descending, efferents. However, this is not generally observed. In the electroreceptive gymnotoids, periventricular tectal neurons have also descending projections, and more peripheral tectal neurons also project to rostral targets.[89] Furthermore, peripheral tectal neurons (types II, IV, and V) in the nonelectroreceptive filefish *Navodon modestus* project to the pretectum.[147,166] The neurons providing the motor output are spatially patterned within one tectal hemisphere where largely nonoverlapping areas (in the rostrocaudal and mediolateral planes) initiate ipsilateral turning, contralateral turning, or rolling of the eyes and the body.[81]

The cytoarchitectonic and modular organization of the tectum, its segregated multimodal input, and the topographical representation of this input provide a neuronal machinery that appears to be exquisitely designed for integrative orientation tasks, such as object identification and location, and coordinated motor control.

3. Telencephalon

In teleosts, the topology of the telencephalon is highly distorted.[172] In all other vertebrate groups, the telencephalic hemispheres develop by paired evagination and thickening of the most rostral embryonic neural tube and each hemisphere contains in its center a lateral diverticulum of the telencephalic midline ventricle. In ray-finned fishes (most pronounced in teleosts), the roof plate of the embryonic telencephalon extends laterally with the effect that the paired dorsal parts of the alar plates forming the hemispheric walls (the prospective pallium) roll out lateroventrally, a process called eversion. In addition to major translocations of pallial cell masses, eversion has the consequence that the telencephalon is covered by a thin (roof plate-derived) tela which ensheats the lateral ventricles. This developmental event makes it very difficult to infer from the adult topology of teleostean telencephalic cell masses alone their homologous structures in other vertebrates, though some advances due to hodology and immunohistochemically established distribution of neuroactive substances have been made recently.

The smell-brain theory on vertebrate telencephalic evolution proposes that (secondary) olfactory input dominates most, if not all, telencephalic areas in cartilaginous and ray-finned fishes and that additional sensory systems invade the telencephalon step-by-step only in amniotes. Ebbesson and Schroeder[55] showed that this is not true in cartilaginous fishes, and similar findings followed for ray-finned fishes. Thus, secondary olfactory information does not dominate the telencephalon in these two major groups of fishes; olfaction is only

represented in limited pallial areas (mostly the lateral pallium) and in some subpallial regions (see Section II.A.1).

Indeed, comparative research during the last 25 years has shown that there are more similarities in the organization of the teleostean and tetrapod telencephalon than previously believed:[163,170,172,176,184,187,228]

1. Most sensory systems reach the telencephalon in teleosts and there are strong reciprocal interconnections between diencephalic and telencephalic sensory zones.
2. There are ascending activation systems to the teleostean telencephalon, such as the noradrenergic locus coeruleus,[61] the serotoninergic raphe nuclei,[104] and possibly a dopaminergic substantia nigra-like system (see below), in addition to other inputs arising in the reticular formation.
3. In teleosts, two major telencephalic divisions are present; the area ventralis telencephali is organized into nuclei, while the area dorsalis telencephali exhibits large zones with a high degree of migration and sometimes even lamination.

Further differences in histology, degree of cytoarchitectonic differentiation, sensory input and neurotransmitter distribution are also reminiscent of pallial vs. subpallial telencephalic cell masses of tetrapods and other vertebrates, although many problems remain to be resolved regarding the homology of particular teleostean nuclei or zones.

It is amazing that the teleostean telencephalon has these features which were once believed to be characteristic only of the more highly evolved telencephalon — the ultimate integrative center — of tetrapods, especially of mammals. However, great difficulties remain to be resolved with respect to the recognition of homology between specific telencephalic areas, e.g., with regard to the dorsal pallium, hippocampus, or septum homologue in teleosts.[172,184] Despite the topological distortion caused by eversion, connectional and immunohistochemical data have led to the recognition of likely candidates for the teleostean lateral pallium (olfactory cortex) and striatum. Since the posterior zone of area dorsalis telencephali is the strongest pallial recipient of secondary olfactory projections in all teleosts examined, it probably represents the lateral pallium of other vertebrates. In *Polypterus senegalus*, a nonteleost (cladistian; Figure 1B) ray-finned fish, the dorsal nucleus of area ventralis displays substance P-containing neurons which project to catecholaminergic (probably dopaminergic) ventral mesencephalic/posterior tubercular cells. The latter, in turn, project back to the (substance P-containing) dorsal nucleus of area ventralis.[199] Also in teleosts, dopaminergic[60,205] and substance P-immunoreactive cells[215] have been identified in comparable locations. This indicates the presence of a system similar to the striatonigral system of tetrapods also in actinopterygians.

Two fundamental differences in forebrain organization between teleosts and other vertebrates exist. A first is the developmental eversion of the telencephalic hemispheres which uniquely applies to ray-finned fishes. Its significance has yet to be determined. A second is the predominance of the posterior tuberculum vs. the dorsal thalamus in relaying sensory information to the telencephalon in teleosts vs. tetrapods (see below). Clearly, we are only at the beginning of fully understanding the differences as well as the similarities in telencephalic organization between teleosts and other major vertebrate groups.

III. THE COMPARATIVE CONTEXT: TELEOSTS AMONG OTHER FISHES AND TETRAPODS

The circuitry of the optic tectum, cerebellum, and telencephalon is surprisingly similar in teleosts and other vertebrates. This also applies to the teleostean sensory systems, in which all the ascending pathways via the diencephalon to the telencephalon have been established. Although the homology of sensory pathways between teleosts and tetrapods is not certain in each single case, the degree of similarity is nevertheless of great functional interest.

Comparable to mammals, in the teleostean olfactory system a tertiary olfactory pathway reaches the pallium via the diencephalon in addition to the more direct, secondary olfactory input (Figure 3). Also, the teleostean visual system exhibits a direct retino-thalamofugal and an indirect retino-tecto-thalamofugal system via the dorsal thalamus (Figure 4A). However, both may be terminating in the subpallium and not in the pallium, in contrast to amniotes. The sensory systems ascending in the lateral longitudinal fascicle, i.e., audition (Figure 8), mechanoreception (Figure 6), and electroreception (Figure 7) are comparable to the lateral lemniscal system of tetrapods. Gustation in teleosts reaches the diencephalon and telencephalon via a secondary gustatory nucleus (Figure 9) which is comparable to the parabrachial nuclear region of mammals. Finally, teleosts possess a direct spinal ascending somatosensory system comparable to the mammalian anterolateral (protopathic) system in addition to indirect spinal ascending projections which are relayed at the obex level (Figure 10), comparable to the mammalian medial lemniscal (epicritic) system.

It was long thought that ascending sensory systems reaching the telencephalon are exclusively characteristic for amniotes or even mammals only. The data summarized here suggest that there is a pattern of ascending sensory pathways to the telencephalon common to tetrapods and actinopterygians. Since tetrapods are sarcopterygians which form the sister-group of actinopterygians (Figure 1A), information on cartilaginous fishes holds the promise to reveal the plesiomorphic condition of ascending sensory systems in gnathostomes. Ebbesson and Schroeder[55] made the important discovery that the telencephalon of cartilaginous fishes receives (unspecified) thalamic inputs in addition to restricted olfactory projections. Later, the visual system of cartilaginous fishes was demonstrated to include of a retino-thalamofugal and a retino-tecto-thalamofugal system,[131,132,182] as is the case in teleosts. Cartilaginous fishes also have a lateral lemniscal system carrying auditory, mechanosensory, and electrosensory signals towards the telencephalon.[7,30,31,32,37,47] Further, directly ascending spinal somatosensory pathways exist up to the dorsal thalamus in chondrichthyans, though the presence of an indirect somatosensory system relayed at the obex level is unclear in these fishes.[219] Ascending gustatory pathways have not been investigated in cartilaginous fishes.

However, a great difference between teleosts and tetrapods is that the predominant diencephalic targets of teleostean ascending sensory projections are not in the dorsal thalamus, but in the posterior tuberculum, mostly in the preglomerular nuclei. Specific sensory preglomerular nuclei certainly exist for the mechanosensory (Figure 6), the electrosensory (Figure 7), and the gustatory systems (Figure 9). There is also a preglomerular nucleus relaying visual information from tectum to telencephalon at least in some teleosts (Figure 4B). Somatosensory information, too, may be relayed in the preglomerular region.[67] Furthermore, these preglomerular nuclei — and not the dorsal thalamic ones — provide the major diencephalic input to the pallial zones of the area dorsalis telencephali. Also, the preglomerular nuclei in teleosts clearly display a higher degree of cytoarchitectonic differentiation and interspecific variation compared to the dorsal thalamus. Thus, the functional similarities between the teleostean preglomerular region and the amniote dorsal thalamus are striking: both make up large proportion of the diencephalon, are subdivided into many nuclei associated with specific sensory systems, and further, most of them have reciprocal connections with the telencephalon.

In order to reveal the plesiomophic condition of diencephalic sensory targets, cartilaginous fishes again need to be considered. It is unclear, which diencephalic region is involved in audition[141] in chondrichthyans, although an autoradiographic deoxyglucose study suggests that it is the dorsal thalamus.[47] The ascending mechanosensory system reaches the dorsal thalamus as well as the region lateral to the posterior tuberculum.[26,27] Electroreception, on the other hand, does not run via the dorsal thalamus, but is represented in a ventral nucleus lateral to the posterior tuberculum and in a hypothalamic nucleus, and both nuclei project to the telencephalon.[29,63,213,214,218] These data in cartilaginous fishes suggest that a dual innervation

of the diencephalon (dorsal thalamus/posterior tubercular region) by at least some ascending sensory systems is the plesiomorphic pattern for gnathostomes. Furthermore, it may be a plesiomorphic gnathostome pattern that hair cell sensory organs in the labyrinth (audition, vestibular sense) are represented in the dorsal thalamus and the remaining hair cell sensory organs (mechanoreception, electroreception) are present in the posterior tubercular region. If so, the evolutionary loss of the latter sensory systems in amniotes may directly explain the dominance of the dorsal thalamus as the diencephalic sensory region in amniotes.

Except for the long palliospinal and palliopontine tracts which represent independently evolved, apomorphic characters of mammals and birds,[206] the motor and premotor systems of teleosts also resemble those of tetrapods. As in mammals, descending spinal projections in teleosts originate in all divisions of the reticular formation, in the caudal (inferior) raphe region, in vestibular nuclei, and even in the nucleus ruber (Figure 11). Also comparable to tetrapods are the tectal and cerebellar efferents to the reticular formation and the contralateral cerebellar input to nucleus ruber in teleosts. However, the forebrain control centers of teleostean spinal descending systems are less clear compared to tetrapods. In amniotes, a telencephalo-pretecto-tectal circuit exists (in birds via the lateral spiriform nuleus, in other reptiles via the nucleus of the posterior commissure[144,200]). In teleosts, none of the pretectal nuclei that project to the tectum receive a telencephalic input, but the tectum itself does so (Figure 13). In birds — but not in other reptiles — a distinct telencephalo-pretecto-cerebellar circuit runs via the medial spiriform nucleus.[109] Comparable to this indirect telencephalo-cerebellar system in birds, three such systems have evolved independently in various teleostean taxa.[235] Even more than in the case of the sensory systems, studies in cartilaginous fishes are badly needed in order to understand the plesiomorphic condition of multisynaptically descending ("extrapyramidal") systems in gnathostomes.

Modern comparative research has fundamentally changed our view of vertebrate CNS evolution: the emergence of a largely conservative bauplan of vertebrate CNS organization has replaced the metaphor of the CNS slowly climbing up the ladder of progress from fishes to humans.

ABBREVIATIONS TO ALL FIGURES

A: anterior thalamic nucleus, AO: anterior octaval nucleus, Au: auricle, BO: olfactory bulb, BS: brainstem, C: nucleus corticalis, Ce: cerebellum, CCe: corpus cerebelli, CON: caudal octavolateralis nucleus, CM: corpus mamillare, CN: lateral cuneate nucleus, CP: central posterior thalamic nucleus, CPN: central pretectal nucleus, D: dorsal telencephalic area, Dc, Dd, Dl, Dm, Dp: central, dorsal, lateral, medial, and posterior zones, respectively, of D, Di: diencephalon, Dlp: posterior part of Dl, DO: descending octaval nucleus, DP: dorsal posterior thalamic nucleus, DT: dorsal tegmental nucleus, EG: eminentia granularis, ELL: electrosensory lateral line lobe, EW: perinuclear cells of Edinger-Westphal nucleus, FLo: facial lobe, G: nucleus glomerulosus, I: intermediate superficial pretectal nucleus, IMRF: intermediate reticular formation, IO: inferior olive, IR: inferior raphe, IRF: inferior reticular formation, LB: nucleus lobobulbaris, LC: locus coeruleus, LCe: caudal cerebellar lobe, LI: hypothalamic inferior lobe, LLN: lateral line nerves, LT: nucleus of the lateral thalamus, M: magnocellular superficial pretecal nucleus, (except in Figure 11, where M: Mauthner cell), MaO: magnocellular octaval nucleus, MD: mediodorsal nucleus of torus semicirularis, MFN: medial funicular nucleus, MO: medulla oblongata, MON: medial octavolateralis nucleus, NAOD: dorsal accessory optic nucleus, NAOV: ventral accessory optic nucleus, NCW: nucleus of the commissure of Wallenberg, NDT: nucleus of the descending trigeminal root, NF: nucleus of the medial longitudinal fascicle, NI: nucleus isthmi, NIII: oculomotor nucleus, NL: lateral nucleus of torus semicirularis, NLL: nucleus of the lateral lemniscus, NLV: nucleus lateralis valvulae, NP: nucleus paracommissuralis, NR: nucleus ruber, NRL: lateral reticular nucleus,

NT: nucleus taeniae, OM: olfactory mucosa, ON: optic nerve, P: parvocellular superficial pretectal nucleus, pDm: posterior part of Dm, PE: preeminential nucleus, PGd, PGl, PGr, PGv: dorsal, lateral, rostral, and ventral preglomerular nuclei, respectively, PL: nucleus perilemniscularis, PM: magnocellular preoptic nucleus, PMg: gigantocellular part of PM, PO: posterior pretectal nucleus, PPa: anterior part of parvocellular preoptic nucleus, PPd: dorsal periventricular pretectal nucleus, PPp: posterior part of parvocellular preoptic nucleus, PT: posterior tuberal nucleus, PTh: posterior thalamic nucleus, R: retina, RT: rostral tegmental nucleus, S: secondary olfactory peduncle, SC: spinal cord, SG: secondary gustatory nucleus, SO: secondary octaval population of McCormick and Hernandez (1996), SRF: superior reticular formation, STN: isthmic primary sensory trigeminal nucleus, T: nucleus tangentialis, Tel: telencephalon, TeO: optic tectum, TG: tertiary gustatory nucleus, TL: longitudinal torus, TLa: torus lateralis, TPp: periventricular nucleus of posterior tuberculum, TS: torus semicircularis, TSc: central nucleus of torus semicircularis, TSvl: ventrolateral nucleus of torus semicircularis, V: ventral telencephalic area, Va: valvula cerebelli, Vam: medial leaf of valvula cerebelli, Vd: dorsal nucleus of ventral telencephalic area, VL: ventrolateral thalamic nucleus, VLo: vagal lobe, VM: ventromedial thalamic nucleus, VT: ventral tegmental nucleus.

ACKNOWLEDGMENTS

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