The Central Nervous Organization of the Lateral Line System

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Abbreviations often used in text:

ALLN	anterior lateral line nerves
CON	caudal octavolateralis nucleus
Dc/Dd/Dl/Dm	central/dorsal/lateral/medial zones of dorsal (pallial) telencephalon
DON	dorsal octavolateralis nucleus
ELL	electrosensory lateral line lobe
EOD	electric organ discharge
LMN	lateral mesencephalic nucleus
MON	medial octavolateralis nucleus
MV	medioventral toral nucleus (mormyrids)
NE	exterolateral toral nucleus (mormyrids)
NL	lateral toral nucleus (mormyrids)
PCT	posterior central thalamic nucleus
PEd	dorsal preeminential nucleus
PGLd	dorsal division of lateral preglomerular nucleus
PLLN	posterior lateral line nerves

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PLT	posterior lateral thalamic nucleus
TS(c,l)	torus semicircularis (central, lateral, etc)
VON	ventral octavolateralis nucleus

1 Introduction

In the present chapter, the central neuroanatomy of the mechanosensory and electrosensory lateral line system in craniates will be considered in each craniate/vertebrate taxon (Fig. 1). Both sensory systems will be dealt with because the neuroanatomy of the mechanosensory lateral line system can not be treated reasonably when ignoring that of the electrosensory system. These two sensory systems share commonalities to a degree that no other two sensory systems do (even including the octaval system of the inner ear). Among those commonalities are that (1) the developmental origin of peripheral receptors in the skin as well as that of the cranial nerve ganglion cells is from the same source, that is, the lateral line placodes (embryonic epidermal thickenings with neurogenic potential), (2) the primary sensory neurons (cranial nerve ganglion cells) may populate the same ganglia and their peripheral fibers may course in the same lateral line nerves, (3) the central fibers of lateral line ganglion cells all terminate in the anterior alar plate of the rhombencephalon, the so-called octavolateralis area.

The hierarchical synaptic chain of ascending pathways in the central nervous system - from the rhombencephalon to the telencephalon - further illustrates the close developmental and evolutionary relationship of these two functionally distinct sensory systems. As mentioned, primary lateral line centers always involve rhombencephalic nuclei in the octavolateralis area (dorsal octavolateralis nucleus for the electrosensory system; medial octavolateralis nucleus for the mechanosensory system) and projections from these nuclei reach a caudal part of the midbrain roof (torus semicircularis). In the diencephalon, two areas are involved, the posterior tuberculum (preglomerular area in teleosts) and/or the dorsal thalamus, and sometimes in addition hypothalamic centers. Projections to the telencephalic pallium (in particular the medial pallium, i.e., the hippocampus homologue) arise only from the posterior tubercular and/or dorsal thalamic lateral line related nuclei.

Additionally, some basic information on the octaval system will be given, mainly because the new concept of the octavolateralis area (see below) cannot be gathered without information on at least the location of the primary sensory octaval nuclei in the octavolateralis area, which are therefore also depicted in addition to lateral line centers in many figures. Also, cases of limited overlap of primary octaval and lateral line nerve projections in mechanosensory and octaval nuclei will be addressed (see also Chapter by Braun & Sand). However, the ascending octaval pathways will only be touched when they converge with lateral line pathways.

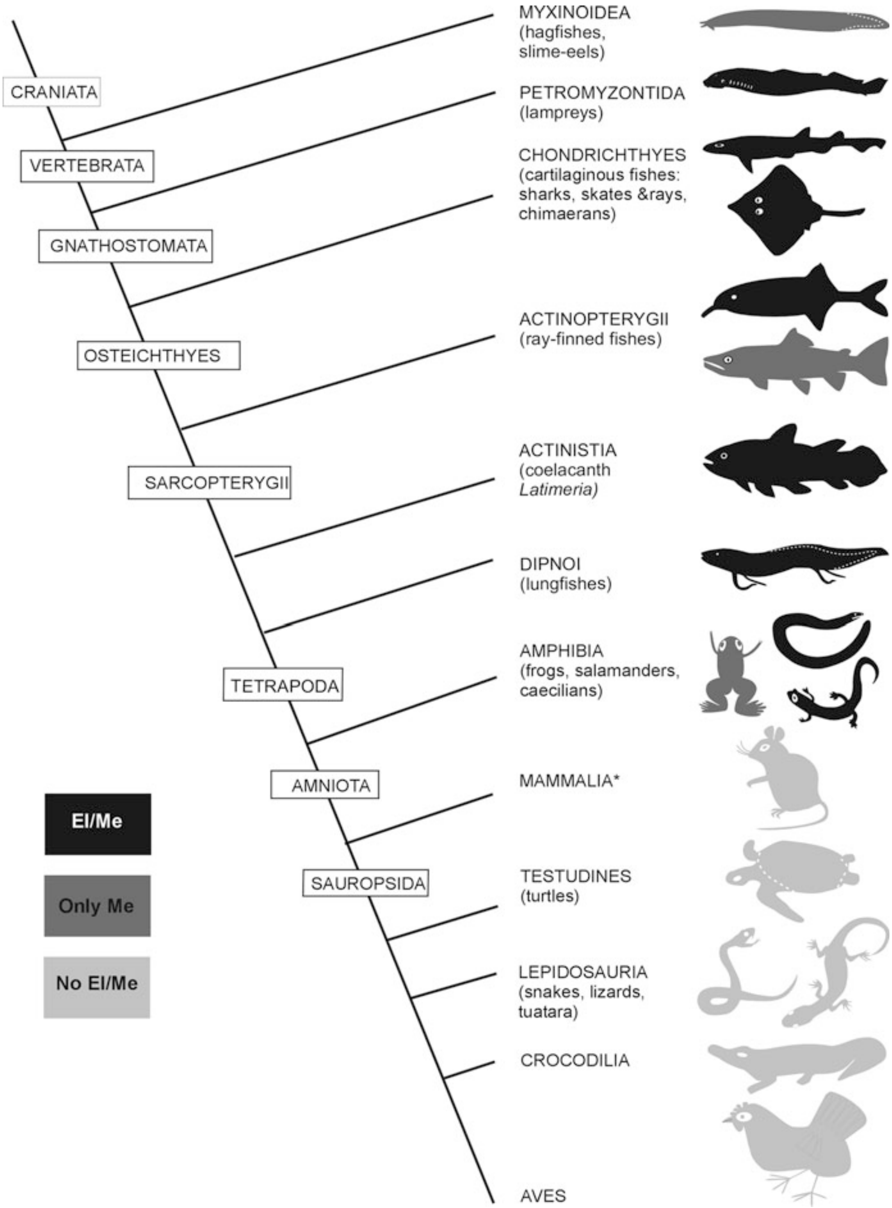

Fig. 1 Cladogram of extant craniate groups with distribution of lateral line mechano- (Me) and electroreception (El) indicated. All groups have inner ear vestibular systems. * Both monotremes (*Platypus*; Scheich et al., 1986) and some eutherians (Guiana dolphin; Czech-Damal et al., 2011) independently acquire trigeminal nerve innervated electroreception, which is convergent to electroreception described in this chapter

This detailed analyis of the lateral line system will start with agnathans and proceed to cartilaginous and ray-finned fishes. Some ecological and paleontological information is given, in particular for agnathans, in order to understand possible regressive phenomena in the lateral line system. From this, it may be concluded that the mechanosensory lateral line is ancestral for craniates, and electroreception is ancestral for vertebrates (Fig. 1). Basal ray-finned fishes share a lot of commonalities with cartilaginous fishes, whereas teleosts (derived ray-finned fishes) lose the electrosensory system, only to have it re-evolve various times. These electrosensory teleostean taxa (silurids, gymnotoids, mormyrids) will be treated separately and, thus, the reader may easily acquire the general phylogenetic story on the mechanosensory lateral line system by skipping these sections and directly proceed to lobe-finned fishes (which include amphibians).

As mentioned, the octavolateralis area is in receipt of lateral line and octaval (VIII) nerve projections. Ironically, it had been recognized historically that the octavolateral (or acousticolateral) area consists of dorsal, medial and ventral nuclei (for example: Larsell, 1967; see discussion in Northcutt, 1986a; McCormick, 1992). Nevertheless, the predominant view into the early 20th century, based on normal histology, has been that input from these nerves to the octavolateralis area is strongly overlapping. Modern tracing methods developed around 1980, in particular the use of horseradish peroxidase (HRP) as an *in vivo* neuronal tracer and its subsequent histochemical visualization (Mesulam, 1982), led to a revision of this view because antero- and retrogradely labeled axonal projections and terminal fields could now be demonstrated more reliably than for example with silver degeneration methods. Thus, largely non-overlapping primary projections of octaval and lateral line mechanosensory and electrosensory projections were shown to reach ventral, medial (intermediate) and dorsal nuclei, respectively (as will be detailed below). A closely related idea is that the inner ear arose phylogenetically as an internalization of part of the peripheral lateral line system (acousticolateralis or octavolateralis hypothesis; see Chapter by Braun & Sand). The phyletic distribution of these sensory organs in craniates together with developmental studies then indicated that the mechanosensory lateral line organs and the inner ear are equally old among craniates (Northcutt, 1986a). However, this is only part of a more fundamental change in how neurobiologists began to view the lateral line system, synthesizing information coming from neuronal tracing, electrophysiology and developmental studies, culminating in the recognition of the mechansensory (and electrosensory) lateral line system as a functionally distinct sensory system on all investigated levels: phylogeny, neuroanatomy, neurophysiology, and development (compare Coombs et al., 1989). Today it is widely accepted that the lateral line nerves are cranial nerves in their own right characterized by discrete embryonic origins (placodes different from the otic one), as well as by distinct adult sensory organs (i.e., neuromasts and electroreceptors) and sensory ganglia, as well as primary central projection areas, with all these characters being separate from those of other cranial nerves, such as the trigeminal, vagal or octaval nerves (McCormick, 1982; Northcutt, 1989).

2 The Agnathan Condition: Myxinoids and Petromyzontids

The current consensus based on phenotypic character analysis is that agnathans are not monophyletic (i.e., they do not share a single last common ancestor, but see discussion of conflicting molecular data in Janvier, 2008). Hagfishes are the sistergroup of vertebrates (lampreys and gnathostomes) and lampreys are the sistergroup of gnathostomes (jawed vertebrates; Fig. 1). Recent systematic accounts on fossil (†) and extant agnathan relationships (Janvier, 2008) propose lampreys and soft-bodied euphaneropids (†) as sistergroup to all other known fossil ostracoderms (e.g., osteostracans, heterostracans, anaspids; characterized by a heavy dermoskeleton) and all gnathostomes. Osteostracans (†) represent the sistergroup of gnathostomes, which makes fossil ostracoderms non-monophyletic. However, unlike in previous suggestions (Northcutt, 1996), lampreys are not closely related to anaspids (†). Consequently, the absence of a dermal armor (exoskeleton) and presence of a cartilaginous endoskeleton (cranium) in modern lampreys (and hagfishes) may not be interpreted as regressive, but represent the ancestral craniate condition. However, this does not preclude regressive processes in other organ systems in extant agnathans (see below).

Hagfishes (Myxinoids) are the only known extant non-vertebrate craniates. They are highly specialized to live on deep ocean shelfs (benthic/endobenthic) and have predominantly chemosensory orientation (Braun 1996, 1998). Their mode of life as scavengers on large bodied vertebrates (including whales) can obviously not be ancestral as fossil agnathans are the first craniates originating in the Paleozoic (Ordovician). In line with this, hagfish fossil record only dates back to the Carboniferous. Interestingly, newer reports indicate that hagfish predation on small invertebrates does occur (discussed in Braun & Northcutt, 1998), more likely representing the ancestral agnathan mode of life. Thus, hagfishes likely show a mixture of primitive and secondary simplified (regressive) characters (Braun, 1996; Northcutt, 1996; Braun & Northcutt, 1997). The lateral line system illustrates this nicely. Pacific (eptatretid) hagfishes have epidermal grooves in the lateral head that contain sensory cells with a kinocilium resembling vertebrate hair cells. However, hagfish hair cells do not show the vertebrate-typical graded (polarized) stereovilli (with the longest ones toward the kinocilium) and hair cells are not arranged into differently oriented populations with opposing polarization as in all vertebrate fish species examined (see below and chapter by Chagnaud & Coombs). Eptatretid hair cells also do not group into functional multicellular units (neuromasts) covered by a cupula and are, thus, not sensitive to displacement in one plane in opposing directions as is the case in vertebrates. These lateral line hair cells in pre- and postoptic epidermal grooves of the eptatretid hagfish head are innervated by two anterior lateral line nerves (Braun & Northcutt, 1997) which project centrally to the ipsilateral octavalateralis area (Kishida et al., 1987) in the rostrodorsal medulla oblongata where the lateral line nerve terminal field lies dorsal to the more ventral octaval nerve projection zone (Amemiya et al., 1985).

In contrast, Atlantic myxinid species do not have a lateral line system at all. They live at greater depths than eptatretids and are burrowers in sandy environments. The Pacific eptatretids may also burrow, but remain more often on the sea floor surface even in the resting state (discussed in Braun & Northcutt, 1998). Thus, the absence of a lateral line system in Atlantic myxinids correlates nicely with their burrowing lifestyles that likely interfere with lateral line function. Since Atlantic myxinids are generally interpreted to show more regressive characters than Pacific eptatretids (for example in the eyes; Fernholm & Holmberg, 1975), the presence of a lateral line system in eptatretids suggests that it is ancestral for craniates, whereas its absence in Atlantic myxinids might represent a secondary loss for this group. Moreover, developmental evidence and the high intraspecific variability of lateral line grooves suggest that the absence of true neuromasts in eptatredids may also be regressive (Braun & Northcutt, 1997). In any case, both the lateral line and octaval systems of hagfishes lack efferent octavolateralis cells (i.e., central medullary cholinergic cells synapsing on peripheral receptor cells). There is also no evidence for electroreception in hagfishes (Bullock et al., 1982, 1983). These two absences, together with the lack of lateral line canals, are likely ancestral for craniates. Information on ascending projections of the lateral line system in hagfishes is not available, although it is clear that the highly differentiated, cortically organized pallium (5 layers) of eptatretids receives in addition to extensive olfactory input also diencephalic input of unknown functional significance (Wicht & Northcutt, 1998).

Lampreys (Petromyzontids), the sole extant representatives of agnathan vertebrates (Fig. 1), are now regarded as outgroup of fossil ostracoderms and gnathostomes (see above; Janvier, 2008). Extant adult lampreys are parasitic on large bony fishes and, thus, are not benthic and generally more mobile than hagfishes. Similar to hagfishes, the parasitic lifestyle of lampreys is hardly feasible without large bony fish hosts. Consequently, the lamprey fossil record only dates back to the very late Devonian (during which large bony fishes first evolved) and not the Ordovician-Silurian-Early Devonian, when ostracoderm radiation peaked (Janvier, 2008). Thus, despite the fact that many lamprey characters, in particular regarding the skeleton, have newly been interpreted as being ancestral instead of regressive (see above), lampreys may still show derived features, in particular with regard to their parasitic mode of life.

Unlike hagfish, lampreys have mechanosensitive free (superficial) neuromasts containing polarized sensory cells with one kinocilium and size-graded stereovilli. Within a single neuromast, the kinocilium is either at the rostral or caudal rim of a given hair cell and all hair cells of a neuromast are unified by a cupula. Therefore, neuromasts form a functional unit that has a single axis of best sensitivity in opposite directions (Yamada, 1973; Jörgensen, 1989), a typical feature of the peripheral lateral line system (see below and Chapter by Chagnaud & Coombs). Lampreys furthermore have electrosensitive end buds (which are different from ampullary organs of gnathostomes, see below), and photosensitive multivillous cells (Ronan & Bodznick, 1986; Braun 1996). All of these sensory organs/cells are innervated by cranial nerves that are referred to as lateral line nerves. Neuronal tracing experiments revealed that three anterior lateral line nerve (ALLN) ganglia

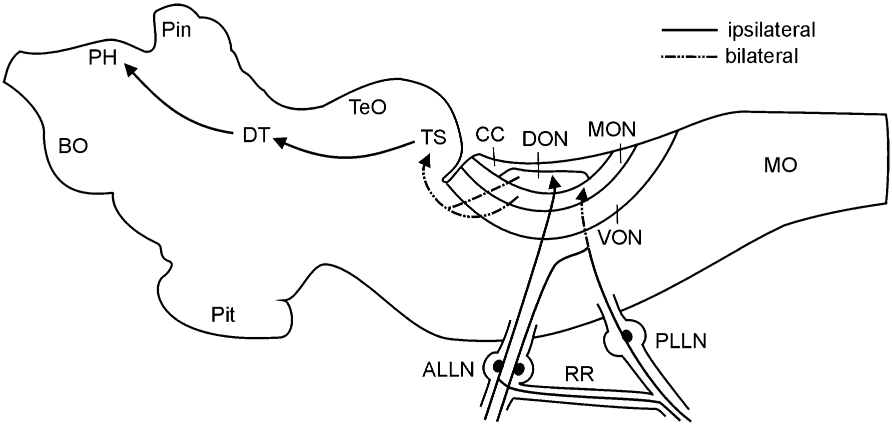

Fig. 2 Schematic lateral view of lamprey ascending lateral line pathways (modified after Northcutt, 1981, see text for more citations). Note that the ventral octaval column contains three octavomotor nuclei (not shown) with descending (spinal) efferent connections. Note that the posterior lateral line nerve ganglion contains only mechanosensory lateral line cells, whereas the anterior ganglia contain additionally electrosensory cells (see text for details). Abbreviations: ALLN anterior lateral line nerves, BO olfactory bulb, CC cerebellar crest, DON dorsal octavolateralis nucleus, DT dorsal thalamus, MO medulla oblongata, MON medial octavolateralis nucleus, PH primordium hippocampi, Pin pineal, Pit pituitary, PLLN posterior lateral line nerve, RR recurrent ramus, TeO optic tectum, TS torus semicircularis, VON ventral octavolateralis column

in lampreys contain primary electrosensory cell bodies (intracapsular and lateral ganglion) and mechanosensory cell bodies (medial ganglion) (Ronan & Northcutt, 1987; Koyama et al., 1990). Their peripheral fibers course in buccal and superficial ophthalmic (both modalities) and hyomandibular rami (only mechanosensory fibers) to reach sensory organs on the snout and around the eye. The single posterior lateral line nerve (PLLN) ganglion has only mechanosensory ganglion cells innervating the trunk neuromasts. However, electrosensory fibers join the PLLN via a recurrent ALLN ramus to innervate trunk electroreceptors (Fig. 2).

The anterior rhombencephalic alar plate of lampreys represents the octavolateralis area which is segregated into three subdivisions: the dorsal octavolateralis nucleus (DON) receiving electrosensory information, an intermediate or medial octavolateralis nucleus (MON) for mechanosensory lateral line information and a ventral octavolateralis nucleus (VON; Northcutt, 1980a, 1981) for octaval information (Fig. 2). The DON and MON are covered by a molecular layer which may correspond to the cerebellar crest of gnathostomes (see below). Contralateral primary mechanosensory lateral line projections to the MON are unique for lampreys. Upon crossing brain sides, mechanosensory fibers terminate also in the transverse ridge (traditionally erroneously recognized as cerebellar corpus) forming the anterior border of the rhomboid groove. This ridge may be comparable to a part of the vestibulo-lateral cerebellar lobe (auricles of cartilaginous fishes, eminentia granularis of bony fishes; see below). A peculiarity of the lamprey electrosensory projection to the DON is that giant terminals are found in the rostral and caudal DON, but only small ones in between, which is possibly related to the processing of temporal or intensity features of the stimulus, respectively (Kishida et al., 1988; Koyama et al., 1993).

In addition to this general segregation of modalities in the lamprey primary sensory centers, there is some overlap of mechanosensory and octaval projections in the dorsal VON and ventrolateral MON (Koyama et al., 1989). The mechanosensory inputs are somatotopically organized in MON (for further details, see Chapters by Chagnaud & Coombs and Bleckmann & Mogdans). There are no efferent octavolateralis cells in the lamprey mechanosensory lateral line system, as opposed to the octaval system (Koyama et al., 1989). Also larval lampreys (ammocoetes) possess both a mechano- and electrosensory lateral line system - somewhat surprisingly in view of their burrowing, filter-feeding lifestyle (Ronan, 1988; González & Anadón, 1992; Gelman et al., 2007). According to the basal systematic position of lampreys (Janvier, 2008), the absence of lateral line canals may be ancestral for craniates. However, lateral line canals are clearly present in the heavy bony armors of most fossil ostracoderm groups and, thus, predate gnathostomes (Northcutt, 1989).

Modern tracing experiments furthermore established that the lamprey torus semicircularis, typically located in the ventroposterior division of the midbrain alar plate (Iwahori et al., 1996), receives bilateral input from the DON and MON (but none from VON) and has in turn strong ipsilateral projections to dorsal and ventral thalamus (Gonzàlez et al., 1999). However, projections from MON (mechanosensory lateral line) and DON (electrosensory) pathways have not been traced separately. Furthermore, thalamic nuclei project to the ipsilateral pallium (the so-called primordium hippocampi; Polenova & Vesselkin, 1993). Evoked potential and single unit electrophysiology revealed electrosensory responses from the DON, torus semicircularis, and optic tectum with increasing latencies (Bodznick & Northcutt, 1981), supporting the anatomical data on the synaptic organization of ascending lateral line pathways. However, comparable physiological information on lateral line mechanosensation is not available and, thus, the case for parallel processing of modalities in the lamprey lateral line system has not been fully made. Also, because physiological information does not exist for thalamic and telencephalic levels, it is not known for certain whether lateral line information reaches forebrain levels.

3 Cartilaginous Fishes: Basal Extant Gnathostomes

Chondrichthyans (cartilaginous fishes) comprise elasmobranchs, which include sharks as well as skates and rays (batoids), and holocephalans (chimaeras, e.g., ratfishes); together, these fishes represent the extant gnathostome outgroup to the remaining vertebrates (Fig. 1). The following findings are compiled from various shark, skate and ray species and are quite comparable between these groups at least regarding the primary central lateral line nerve projection zones. The tracing data stem mostly from Fink-Heimer silver degeneration and HRP experiments.

Elasmobranchs have three anterior lateral line nerve (ALLN) ganglia giving rise to peripheral superficial ophthalmic, buccal and external mandibular rami. These rami innervate canal neuromasts, pit lines with free (superficial) neuromasts and ampullary electrosensory organs of the head (ampullae of Lorenzini). In addition, a PLLN ganglion gives rise to a single nerve that innervates only mechanoreceptors (neuromasts) on the trunk (McGready & Boord, 1976; Boord & Campbell, 1977; Koester, 1983). The central ALLN fibers segregate into a dorsal root containing the electrosensory fibers (Bodznick & Northcutt, 1980) and a ventral root with mechanosensory fibers; the PLLN root is solely mechanosensory (Koester, 1983; Puzdrowski & Leonard, 1993; Smeets 1998). The dorsal root projects to the DON, the ventral and posterior roots to the MON (Fig. 3). Single lateral line fibers typically bifurcate into an anterior and posterior branch within the MON and DON. Additional spatially segregated mechanosensory projections reach the vestibulo-cerebellum (the lateral granular mass and a more medial area of the auricular lower lip; Koester, 1983, Puzdrowski & Leonard, 1993). Both MON and DON are covered by a molecular layer, the crista cerebellaris (Fig. 3). Purkinje-like cells (also called multipolar or crest cells) in DON/MON are located at the periphery towards the cerebellar crest and their dendrites extend into both cerebellar crest and deep parts of DON/MON, where various other cell types are present. Furthermore, auricular granule cells project tangentially into the cerebellar crest of MON (from the lateral granular mass) and of DON (from the dorsal granular ridge; compare with Figs. 3, 4). The cerebellar crest also contains GABAergic stellate cells and, thus, resembles the cerebellar molecular layer (Koester, 1983; Smeets, 1998), although the Purkinje-like crest cells are not GABAergic (Duman & Bodznick, 1997). The noted parallel fiber input from cerebellar granule cells provides proprioceptive/electrosensory input to DON and proprioceptive/auditory/mechanosensory input to MON cerebellar crest (Bodznick and Boord, 1986; Boord & Montgomery, 1989; Conley & Bodznick, 1994) and likely acts in the context of eliminating self-generated (reafferent) signals from the relevant external sensory input (Montgomery et al., 1995; Bell et al., 1997). The elasmobranch ventral octavolateralis area is separated into five distinct nuclei, an anterior, a magnocellular, a descending, a periventricular and a posterior nucleus all of which receive octaval projections (Boord & Roberts, 1980; Northcutt, 1981; Barry, 1987).

Both electroreceptors and lateral line mechanoreceptors are topographically represented within the elasmobranch primary sensory nuclei. Anterior lateral line nerve mechanosensory fibers project into the medial, those from the PLLN into the lateral MON (Fig. 3; Koester, 1983; Puzdrowski & Leonard, 1993). Moreover, diverse ALLN branches (see above) and, therefore, the peripheral distributions of lateral line receptor organs, are somatotopically represented in primary sensory nuclei, in particular the electrosensory terminals in the entire DON, and to a less strict degree the mechanosensory terminals within the medial MON (Bodznick & Schmidt, 1984; Puzdrowski & Leonard, 1993). This somatotopy translates roughly

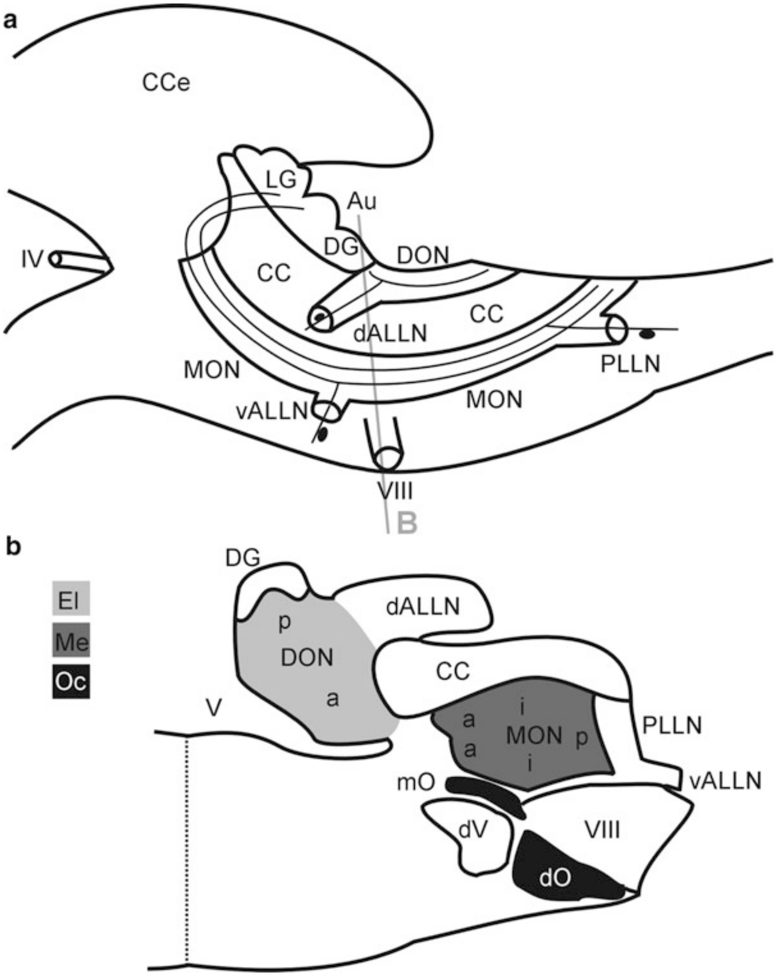

Fig. 3 Lateral line and octaval nerves and octavolateralis area in the medulla oblongata of the lesser-spotted dogfish *Scyliorhinus canicula* (modified after Boord & Roberts, 1980). (**a**) Schematic lateral view. Note bifurcation of incoming lateral line fibers and medial (vALLN) versus lateral (PLLN) segregation of mechanosensory lateral line fibers (see text). (**b**) Schematic transverse section through right side of dogfish octavolateralis area (section level indicated with gray line in **a**) showing segregation of electrosensory (El), mechanosensory (Me) and octaval (Oc) projections. Note that information on projection (other than octaval) sites and somatotopy is from additional elasmobranch species (see text). Abbreviations: a representation of receptors in anterior body periphery, Au auricle, CC crista cerebellaris, CCe corpus cerebelli, dALLN dorsal root of anterior lateral line nerve, DG dorsal granular ridge of auricle, dO descending octaval nucleus, DON dorsal octavolateralis nucleus, dV descending trigeminal root, i representation of receptors in intermediate body periphery, LG lateral granular mass of auricle, mO magnocellullar octaval nucleus, MON medial octavolateralis nucleus, p representation of receptors in posterior body periphery, PLLN posterior lateral line nerve, vALLN ventral root of anterior lateral line nerve, V fourth ventricle IV trochlear nerve, VIII octaval nerve

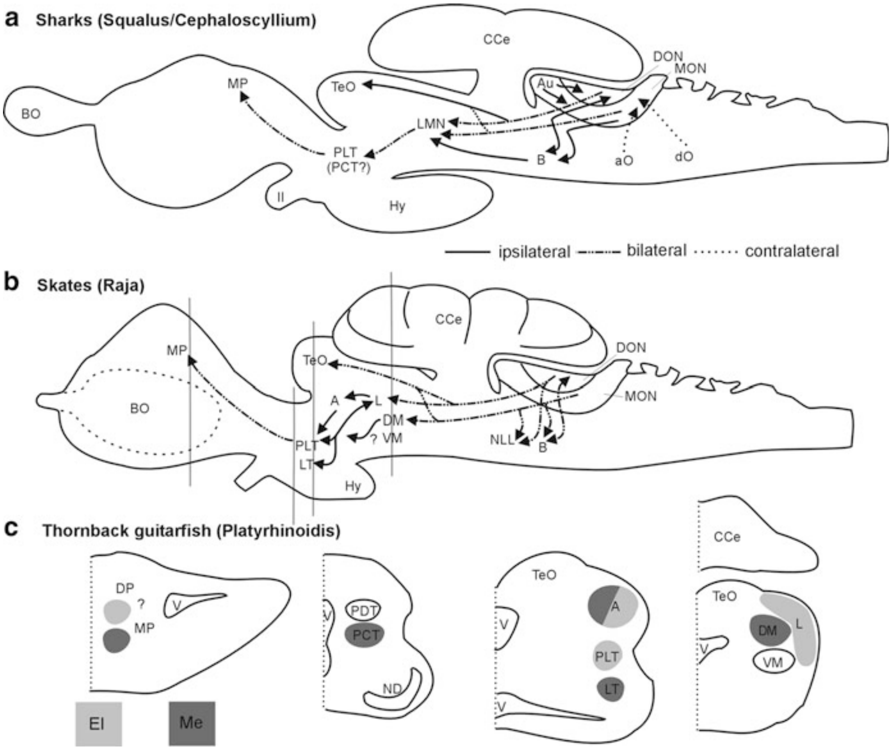

Fig. 4 Schematic lateral views of shark (**a**) and skate (**b**) lateral line ascending pathways. Note that additional strong commissural interconnections between primary sensory lateral line nuclei are not drawn in figures. Also, auricular inputs to batoid DON/MON, as well as DON's ipsilateral afferents from - and contralateral efferents to - a paralemniscal nucleus (Bodznick & Boord, 1986; see text for more citations) are not shown. Note also that *bilateral* means *predominantly contralateral*. (**c**) Schematic transverse views of right brain side of a ray (thornback guitarfish *Platyrhinoidis triseriata*) show electrophysiological identification of electrosensory (El) and mechanosensory (Me) lateral line brain structures (modified from Bleckmann et al., 1987, see text). For convenience, their approximate levels are indicated in the skate lateral view. Note that in *Platyrhinoidis* both PLT/PCT project to the medial pallium (see text for citations). Abbreviations: A anterior mesencephalic nucleus, aO anterior octaval nucleus, Au auricle, B nucleus B, BO olfactory bulb, CCe corpus cerebelli, DM dorsomedial mesencephalic nucleus, DP dorsal pallium, dO descending octaval nucleus, DON dorsal octavolateralis nucleus, Hy hypothalamus, L lateral mesencephalic nucleus of batoids, LMN lateral mesencephalic nucleus of sharks, LT lateral tuberal nucleus, MON medial octavolateralis nucleus, MP medial pallium, ND nucleus diffusus of hypothalamus, NLL lateral lemniscal nucleus, PCT posterior central thalamic nucleus, PDT posterior dorsal thalamic nucleus, PLT posterior lateral thalamic nucleus, TeO optic tectum, V ventricle, VM ventromedial mesencephalic nucleus, II optic nerve

into anteroposterior representations in MON and DON (Fig. 3b), with additional segregation of dorsal versus ventrally located electroreceptors in skates within DON, respectively (Bodznick & Schmidt, 1984). The medial octavolateralis nucleus contains dense cell plates in its center (C1/C2 or nucleus X; discussed in

Puzdrowski & Leonard, 1993) surrounded by mechanosensory terminals. These cell plates represent secondary projection cells of the MON (see below), which is corroborated by the fact that they can be driven by electrical stimulation of ALLN fibers, but not of octaval fibers (Puzdrowski and Leonard, 1993). Nevertheless, there are limited converging projections of octaval and lateral line fibers in the caudal part of the MON and in the magnocellular octaval nucleus, plus more extensive overlaps in the auricles of the vestibulocerebellum (Koester, 1983; Puzdrowski & Leonard, 1993). A very restricted octaval projection to DON (Barry, 1987) is doubtful. Cartilaginous fishes have a cholinergic octavolateralis efferent nucleus located rostral to the visceromotor column (of cranial nerves VII, IX and X) that innervates bilaterally both inner ear and lateral line hair cells, but not electroreceptors (Meredith & Roberts, 1986; Anadón et al., 2000).

Ascending projections arising in DON and MON in elasmobranchs differ somewhat between sharks and batoids and will be examined separately. Studies in sharks exist for a squalomorph shark, the spiny dogfish *Squalus acanthias* (Boord & Northcutt, 1988) and for a galeomorph shark, the carpet or draughtsboard shark (*Cephaloscyllium isabellum*; Boord & Montgomery, 1989). In sharks, both MON and DON have strong reciprocal commissural interconnections. Furthermore, fibers emanating from MON/DON anteriorly form bilateral lemnisci that give rise to the following interconnections. Ipsilateral reciprocal connections with a second order medullary nucleus B exist with DON, but the shark MON has only efferents to nucleus B. In addition, the MON receives contralateral input from both anterior and descending octaval nuclei.

Ascending projections from MON and DON reach bilaterally (predominantly contralaterally) a midbrain region ventral to the optic tectum called lateral mesencephalic nucleus (LMN). The LMN is subdivided into dorsolateral and ventromedial regions which receive electrosensory and lateral line mechanosensory fibers as corroborated with electrophysiology (Northcutt & Bodznick, 1983; Boord & Montgomery, 1989). Both DON and MON fibers also extend further into the ipsilateral or contralateral central zone of the optic tectum, respectively (Fig. 4; Boord & Northcutt, 1988; Boord & Montgomery, 1989). Retrograde tracing in *Cephaloscyllium* showed the origin of mechanosensory projections to LMN in cell plate X, plus in additional multipolar cells in MON (including crest cells, see above; Boord & Montgomery, 1989).

In *Cephaloscyllium*, the LMN projects bilaterally to a diencephalic nucleus termed posterior central thalamus (PCT; Boord & Montgomery, 1989). In *Squalu*s, a more laterally located nucleus, the posterior lateral thalamic nucleus (PLT) projects mostly contralaterally to the telencephalic medial pallium (Smeets & Northcutt, 1987; Fig. 4a). Although an input from LMN to PLT remains undocumented in *Squalus*, it likely represents a diencephalic lateral line nucleus (see below). Thus, it is unclear whether sharks have one or two diencephalic nuclei that relay lateral line information from the midbrain to the telencephalon.

A more differentiated picture for lateral line midbrain and forebrain centers emerged for batoids, i.e., the thornback guitarfish, *Platyrhinoidis triseriata* and two skates of the genus *Raja*. While lateral line pathways have been examined in more detail in skates (Boord & Northcutt, 1982, Bodznick & Northcutt, 1984, Bodznick & Boord, 1986; summarized in Fig. 4b), more electrophysiology exists for *Platyrhinoidis* (see below). In addition to strong reciprocal commissural interconnections, the skate MON and DON give rise to parallel lemniscal mechanosensory and electrosensory pathways, respectively, which course predominantly contralaterally (as in sharks), and reach a lateral lemniscal nucleus and nucleus B (the latter is reciprocally connected with DON). In all batoids, the lateral mesencephalic complex contains four nuclei, lateral (L), dorsomedial (DM), ventromedial (VM) and anterior (A) ones (Fig. 4). Lateral and dorsomedial nuclei are in receipt of electrosensory (DON) and lateral line mechanosensory (MON) inputs, respectively (Boord and Northcutt, 1982), whereas the anterior nucleus is postsynaptic to the lateral one (Bodznick & Boord, 1986). Retrograde tracing from mesencephalic lateral and dorsomedial nuclei reveal that cell plates C1/C2 are the major source of the mechanosensory projection to the dorsomedial nucleus, together with other cells in MON, and that electrosensory projections to the lateral nucleus arise from DON (*Raja*; Barry, 1987). Predominantly ipsilateral connections arise then from the mesencephalic lateral nucleus to the posterior lateral thalamic nucleus (PLT) and to the lateral tuberal nucleus (LT) in the hypothalamus. The posterior lateral thalamic nucleus has also input from the mesencephalic anterior nucleus and projects back to the mesencephalic lateral nucleus (Bodznick & Boord, 1986). The PLT in turn (but not LT) projects to the telencephalic medial pallium (predominantly contralaterally again, thus switching sides). The exact course of lateral line mechanosensory DM output to the diencephalon is unclear in skates. The midbrain area containing lateral line related nuclei of sharks (LMN) and anterior, lateral and dorsomedial/ ventromedial mesencephalic nuclei in batoids may be considered homologous to the torus semicircularis/inferior colliculus of other vertebrates. In batoids, projections from the rhombencephalic lateral lemniscal nucleus (not depicted) and also from MON and DON reach the central zone of the optic tectum (Fig. 4; Boord & Northcutt, 1982; Boord & Montgomery, 1989). Altogether this indicates that the pathways originating in the lateral line mechanosensory MON and the electrosensory DON ascend multisynaptically to the forebrain in cartilaginous fishes. Indeed, electrical stimulation of the DON elicits evoked potential responses in medial pallium and diencephalic PLT (and lateral tuberal nucleus) of the skate (Bodznick & Northcutt, 1984).

The central nervous system of the thornback guitarfish (*Platyrhinoidis*) is well investigated electrophysiologically using either vibrating sphere stimuli (Bleckmann et al., 1989) or PLLN shocks (Bleckmann et al., 1987) to stimulate the mechanosensory lateral line system or rectangular pulse field stimuli for the electrosensory system (Schweitzer, 1983; 1986). Electrosensory stimulation produced evoked responses in the lateral and anterior mesencephalic nuclei and the diencephalic PLT; electrosensory evoked responses were also seen in the dorsal or medial pallium (Fig. 4c; Bullock et al., 1993). Furthermore, omitted stimulus- (i.e., event-) related potentials (likely related to electrosensory expectation) were reported at DON, L and pallial levels. Mechanosensory stimulation resulted in evoked responses in the dorsomedial and anterior mesencephalic nuclei, in the diencephalic posterior central thalamic (PCT) and lateral tuberal (LT) nuclei, and in a ventral medial pallial division (Fig. 4c). Interestingly, these data identify a mechanosensory diencephalic nucleus (PCT) different from the electrosensory PLT, both of which project to the telencephalon in *Platyrhinoidis* (Fiebig & Bleckmann, 1989). Furthermore, both the anterior (A) and lateral (L) mesencephalic nuclei were shown to project to the diencephalic PLT nucleus in this species (Schweitzer and Lowe, 1984). A recent dextran amine tracing study in *Platyrhinodis* confirmed strong PLT projections to the pallium, but did not identify a pallial projecting PCT (Hofmann & Northcutt, 2008). This study also reported a strong input to the mesencephalic lateral (electrosensory) and dorsomedial (mechanosensory) nuclei from a dorsal pallial division and hypothesized that this represents a higher order olfactory connection via the subpallium (area basalis superficialis) converging with lateral line information in the mesencephalon. However, basal forebrain inputs to the pallium may alternatively represent modulatory (non-sensory) input.

Thus, the overall situation speaks for parallel electrosensory and mechanosensory pathways up to telencephalic levels in *Platyrhinoidis*. However, as in skates, the efferents of the (mechanosensory) dorsomedial mesencephalic nucleus are unknown, although they likely reach the diencephalic PCT. In this context, the most pressing questions are whether a diencephalic mechanosensory PCT exists in all cartilaginous fishes separate from an electrosensory PLT and how exactly the two lateral line modalities are represented in the medial/dorsal pallium. Evoked potential and multi-unit responses in the skate medial pallium following either optic nerve, PLLN or DON stimulation revealed largely overlapping electrosensory (although these were slightly deeper) and visual responses, and completely overlapping visual and mechanosensory responses (Bodznick, 1991). In the telencephalic dorsal pallium (nucleus centralis) of the galeomorph nurse shark, visually and trigeminally elicited responses were spatially segregated, suggesting that there may have been an evolutionary switch from multimodal processing in the medial pallium to unimodal processing in the dorsal pallium of cartilaginous fishes (Bodznick, 1991). More focused functional neuroanatomical work in cartilaginous fishes is clearly needed to resolve these important issues.

4 Ray-Finned Fishes: the most Successful Aquatic Bony Fishes

Ray-finned fishes (actinopterygians) underwent a similarly extensive evolutionary radiation as their osteichthyan sistergroup, the sarcopterygians (lobe-finned fishes, including tetrapods; see Section 5). Thus, actino- and sarcopterygians are each comprised of around 25000 extant species. It is peculiar that most actinopterygian taxa, which include over 90% of all extant aquatic vertebrate species, possess only a mechanosensory lateral line system, without an electrosensory counterpart, a fact with no immediate adaptationist explanation. A seminal phyletic analysis of electrophysiological results from the DON in parallel with neuroanatomical studies of the octavolateralis area in all major aquatic craniates has revealed the ancestry of the electrosense within vertebrates and its late phylogenetic loss in tetrapods (Bullock et al., 1982, 1983). However, within actinopterygian fishes, the correlated presence of a DON in the octavolateralis area and evoked potential responses to electric stimuli in DON is only seen in the two most basal actinopterygian groups, polypteriforms (bichirs, reedfish) and chondrosteans (sturgeons and paddlefishes), whereas gars (Lepisosteiformes*)* and bowfins (Amiiformes) - formerly together called holosteans - and the overwhelming majority of more derived (and highly speciose) teleosts lack both electroreceptors and the related central nervous structures, such as the DON. Thus, electroreception which was present in the earliest vertebrates, was lost before teleosts arose in actinopterygian phylogeny and subsequently re-evolved in only a few teleost taxa (see Fig. 1; and Section 4.3). Lateral line central anatomy of electrosensory and non-electrosensory basal ray-finned fishes will be discussed first, followed by consideration of major teleost groups.

4.1 Basal Ray-Finned Fishes

Although the number of discrete lateral line nerve ganglia differs between various ray-finned (actinopterygian) fish groups, there is always an anterior complex of ganglia giving rise to at least a superficial ophthalmic, a buccal and an external mandibular ramus innervating the head periphery and a posterior complex of lateral line ganglia giving rise to nerves innervating the trunk periphery (see review: Northcutt, 1989). For simplicity, only anterior (ALLN) and posterior (PLLN) lateral line nerves will be used below. Basal ray-finned fishes with electroreception (polypteriforms, chondrosteans) resemble cartilaginous fishes in that they carry electrosensory fibers innervating ampullary organs only in the ALLNs, and mechanosenory fibers innervating canal and free (superficial) neuromasts in both ALLN and PLLNs (New & Northcutt, 1984; McCormick, 1989; Piotrowski & Northcutt, 1996). The associated octavolateralis area consequently consists of a dorsal electrosensory column (DON), an intermediate mechanosensory column (MON/plus the caudal octavolateralis nucleus) and a ventral octaval column. The caudal octavolateralis nucleus (CON) lies at the caudal end of MON, is not covered by the cerebellar crest, and is actually present in all gnathostome fishes (McCormick, 1982), including cartilaginous fishes (Puzdrowski & Leonard, 1993). As in elasmobranchs, the actinopterygian MON and DON display Purkinje-like cells towards the cerebellar crest, and various additional, more deeply lying cell types (i.e., granular, fusiform, polygonal), whereas the CON only consists of granular cells (McCormick, 1982; New & Northcut, 1984). The electrosensory nature of the DON was furthermore physiologically confirmed in polypteriforms and chondrosteans (Bullock et al., 1982, 1983). The ventral octaval column in these electrosensory basal actinopterygians contains anterior, magnocellular, descending and posterior octaval nuclei (McCormick, 1982).

The sturgeon ALLN has a dorsal root carrying only electrosensory fibers which terminate in DON and the dorsal granular area of the lateral eminentia granularis, with DON showing evoked responses to electrosensory stimulation (New & Northcutt, 1984; New and Bodznick, 1985). The solely mechanosensory ventral root of ALLN, plus the PLLN, project ipsilaterally to several locations: the MON and its caudal elongation the CON, to the dorsal and rostral eminentia granularis (the actinopterygian vestibulolateral lobe) as well as to the ventral cerebellar corpus (New & Northcutt, 1984). In all these projection sites of the sturgeon lateral line nerves, there is a clear segregation of ALLN/PLLN fibers, with PLLN terminals being dorsal to those of ALLN within each structure. Lateral line nerve projections to the eminentia granularis and corpus cerebelli are bilateral in the sturgeon. In these two cerebellar structures (but not in MON/CON), the most ventral area, presumably the site of octaval nerve terminals (as in bowfins, see below), is always free of lateral line projections. Also, an additional medial part of the ventrolateral granular part of the eminentia granularis receives overlapping ALLN/PLLN projections, and the magnocellular octaval nucleus receives also ALLN input. Sturgeons also have efferent octavolateralis neurons lying at the rostral tip of the visceromotor column. Paddlefishes also have clear anatomical and physiological segregation of an electrosensitive DON and mechanosensitive MON (New & Bodznick, 1985) and they use dense electroreceptors in their rostrum to detect small electric fields emanating from planktonic prey (Wilkens et al., 2002). Electrosensory projections arising from the DON reach the optic tectum, the torus semicircularis and a lateral mesencephalic nucleus (LMN; Hofmann et al., 2002). DON neurons have large receptive fields and - unlike sharks (Section 3) - are not topographically organized (Hofmann et al., 2005). Unlike neurons in DON, those of LMN are activated by electrosensory signals irrespective of orientation and direction, but they also have large receptive fields. Neurons of the optic tectum instead have small receptive fields and are topographically arranged (Chagnaud et al., 2008a, b). The behavioral significance may be that the LMN guides the longer-range orienting response, whereas the optic tectum is involved in the final prey capture.

Although degeneration studies in lampreys, elasmobranchs and teleosts had previously indicated a restriction of octaval projections to the ventral octavolateralis column nuclei (Northcutt, 1981), it was not until the seminal work of Catherine McCormick using modern tracing methodology in the Northcutt laboratory that a new conceptual framework emerged revealing three functional separate longitudinal columns in the vertebrate octavolateral area dedicated to functionally distinct sensory systems (McCormick, 1981a, b, 1982, 1989). Her work concentrated on a pivotal species, the bowfin, *Amia calva*, which is together with gars in a phylogenetic position between teleosts and electrosensory basal ray-finned fishes (i.e., polypteriforms/chondrosteans: see above). As *Amia* lacks an electrosensory system, both a dorsal root of the ALLN and a dorsal column (DON) are absent. Thus, it has only one ALLN root projecting to the intermediate

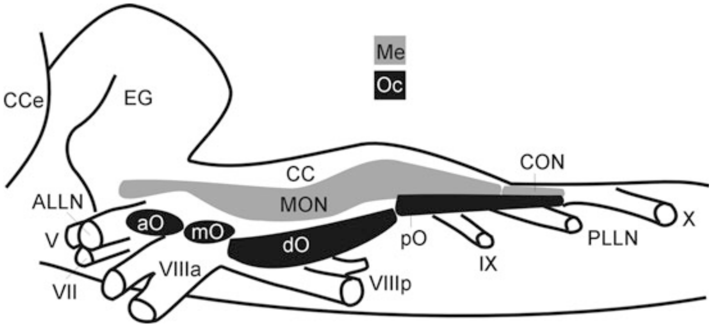

Fig. 5 Schematic lateral view of octavolateralis area in the bowfin *Amia calva* (redrawn after McCormick, 1981b). Abbreviations: ALLN anterior lateral line nerve, aO anterior octaval nucleus, CC crista cerebellaris, CCe corpus cerebelli, CON caudal octavolateralis nucleus, dO descending octaval nucleus, EG eminentia granularis, mO magnocellullar octaval nucleus, MON medial octavolateralis nucleus, PLLN posterior lateral line nerve, pO posterior octaval nucleus, V trigeminal nerve, VII facial nerve, VIIIa, p anterior, posterior parts of octaval nerve, IX glossopharyngeal nerve, X vagal nerve

(MON, CON) column. In addition, there is a ventral column that displays four octaval nuclei (anterior, magnocellular, descending and posterior ones; Fig. 5). These four nuclei are in receipt of octaval nerve projections in *Amia* (McCormick, 1981b), as is the most ventral division of the eminentia granularis. Additionally, sparse octaval nerve terminals were noted in the ventral MON, suggesting a small region of overlap between octaval and mechanosensory input. In contrast, the ALLN root projects heavily into the ventromedial parts of MON and CON, plus the intermediate division of the eminentia granularis, and the PLLN projects into the dorsolateral MON and dorsal eminentia granularis, and sparsely to the magnocellular octaval nucleus, very similar to the situation later reported in chondrosteans (see above; except for the absence of DON and lack of projections to the cerebellar corpus in *Amia*). The Florida gar (*Lepisosteus platyrhincus*) shows highly similar lateral line projections (Song & Northcutt, 1991). The octavolateralis region of *Amia* (Fig. 5) is illustrated because it serves as a blueprint for the teleostean situation and because the sturgeon/polypteriform octavolateral area highly resembles the elasmobranch situation (Fig. 3).

McCormick (1989) later reported MON connections in *Amia*. There are strong commissural interconnections between the two MONs arising from crest cells (McCormick, 1989). The peripheral dendrites of crest cells extend into the cerebellar crest, where they are contacted by parallel fibers issued by granular cells of the eminentia granularis whose axons enter the cerebellar crest tangentially and presumably provide processed lateral line and other higher order sensory inputs. Additionally, the crest cell ventral dendrites receive primary lateral line nerve input, as do deeper lying polygonal and granular cells. In contrast, the CON which receives only lateral line nerve input, consists exclusively of granular cells and does not contribute to descending and ascending connections of the mechanosensory column (McCormick, 1989).

Ascending projections from MON arise in crest cells and deeper polygonal cells and run bilaterally (stronger contralaterally) within the lateral lemniscus (or lateral longitudinal fascicle) anteriorly. Reciprocal connections arise from the lateral lemniscus to the preeminential nucleus, a nucleus ventral to the eminentia granularis. Ascending lateral lemniscal fibers then terminate in a lateral division of the torus semicircularis, in the optic tectum and in a perilemniscal nucleus. Bulk tracer injections into the torus semicircularis show input from this perilemniscal nucleus and confirm MON input. In addition, these tracings reveal strong ipsilateral and weak contralateral ascending toral projections to the diencephalon, that is the central posterior thalamic nucleus (dorsal thalamus) and some divisions of the preglomerular area, in particular the lateral preglomerular nucleus (a migrated part of the posterior tuberculum; McCormick, 1989). These connections are very similar to those seen in non-electrosensory teleosts and their comparative and developmental significance will be discussed in the next section.

4.2 Non-Electrosensory Teleosts

Approximating 25000 species, teleost fishes display great variability in their central nervous systems (Meek & Nieuwenhuys, 1998; Wullimann, 1998; Wullimann and Vernier, 2009) and, thus, a general picture of teleostean central lateral line organization is not easy to give. The most basal teleost clade is that of the osteoglossomorphs which include for example osteoglossids (e.g., the South American Arapaima), as well as African mormyrids (elephantnose fishes) and notopterids (African knifefishes). Elopomorphs (e.g., anguilliform eels, tarpons, ladyfishes) are the next teleost clade, followed by the clupeomorphs (herrings and their relatives). The final clade is formed by the euteleosts which include very large radiations such as the ostaryophysines, for example cyprinids (carps and relatives), silurids (catfishes), or gymnotoids (South American knifefishes). Another huge euteleost clade, the acanthomorphs (perch-type fishes) include sticklebacks, flatfishes, seahorses, triggerfishes, cichlids, basses, and sunfishes, just to name a few. Euteleosts also include salmonids and esocids (pikes). As already pointed out, electroreception is lost in the closest outgroups of teleosts (Amiiformes, Lepisosteiformes) and an analysis within teleosts shows that the sole presence of the mechanosensory modality in the lateral line system becomes, thus, basal for this large group of vertebrates, with only some osteoglossomorphs and silurids/gymnotoids re-evolving electroreception (see next Section). Here, the focus will first be on a discussion of non-electrosensory cyprinid fishes, and information on other non-electrosensory teleosts will follow later.

Being ostaryophysines, cyprinids have a specialized auditory sense. This has drawn scientific attention amongst neurobiologists and the octavolateralis system is, thus, rather well investigated in cyprinids (Webster et al., 1992; Popper & Fay, 1993, 1999). The anterior portion of their swim bladder is mechanically linked to the inner ear via the Weberian ossicles - a series of bones and ligaments derived from most anterior vertebral and rib elements. The swim bladder, as a compressible gas cavity, acts as a sound pressure transducer and - together with the Weberian apparatus – as an amplifier transmitting sound pressure waves to the inner ear where in particular saccular (in goldfish apparently exclusively; Coombs et al., 2010), and maybe lagenar and utricular sensory epithelia are involved in sensing acoustic pressure signals (McCormick & Braford, 1994; Yamamoto & Ito, 2005). The information summarized here is from the common carp (*Cyprinus carpio*) and the goldfish (*Carassius auratus*). The cyprinid octaval nerve projects to the five nuclei comprising the octaval column, i.e., anterior, magnocellular, descending, tangential and posterior octaval nuclei (McCormick & Braford, 1994). The tangential nucleus is an additional solely vestibular nucleus present in teleosts which is absent in basal ray-finned fishes (see Section 4.1). In cyprinids, the dorsomedial part of the descending octaval nucleus has been identified as primary auditory center receiving saccular, as well as lagenar and utricular afferents (McCormick & Braford, 1994; Yamamoto & Ito, 2005). Notably, the large saccular input to this nucleus in the goldfish does not overlap with other inner ear inputs (McCormick & Braford, 1994). Also the dorsocaudal part of the anterior octaval nucleus receives saccular input, but mostly overlapping with all other inner ear inputs (McCormick & Braford, 1994). Descending spinal projections in cyprinids originate in all five octaval nuclei, with the exception of the said acoustically related dorsomedial part of the descending octaval nucleus (Prasada Rao et al., 1987; McCormick & Braford, 1994; Becker et al., 1997). The latter has instead ascending projections to the central nucleus of the torus semicircularis in cyprinids (Echteler, 1984, 1985b; McCormick & Hernandez, 1996), as does the anterior octaval nucleus in the carp in addition (Echteler, 1984, 1985a; Yamamoto & Ito, 2005). The zebrafish, another cyprinid species with relatively small primary chemosensory lobes compared to carp/goldfish, has an additional spinal projection descending from the MON (Becker et al., 1997), whereas in the goldfish, an additional spinal projection originates in the large (primary gustatory) facial lobe (Prasada Rao et al., 1987), indicating that different sensory systems are involved in the control of spinal circuits depending on species-specific sensory specialization. In this context, it is worth noticing that the pair of large Mauthner cells, which initiate hearing induced escape behavior, also receive lateral line input (for more citations and discussion, see Mirjany & Faber, 2011 and Chapter by Braun & Sand).

The cyprinid ALLN and PLLN roots enter the brain at the level of the octavolateralis area (Fig. 6a; Luiten, 1975; Zottoli & van Horne, 1983; Puzdrowski, 1989). Although there is an anterodorsal and anteroventral ALLN root in cyprinids, these together correspond to the ventral ALLN root of basal actinopterygians and, thus, solely contain mechanosensory fibers innervating canal and free (superficial) neuromasts, as does the PLLN (Puzdrowski, 1989; Schmitz et al., 2008). The lateral line nerves project ipsilaterally to the MON and CON, which lie anterior to the large gustatory facial and vagal lobes (Figs. 6a, b). Additional lateral line projections reach the cerebellar granular eminence and transgress even slightly into the

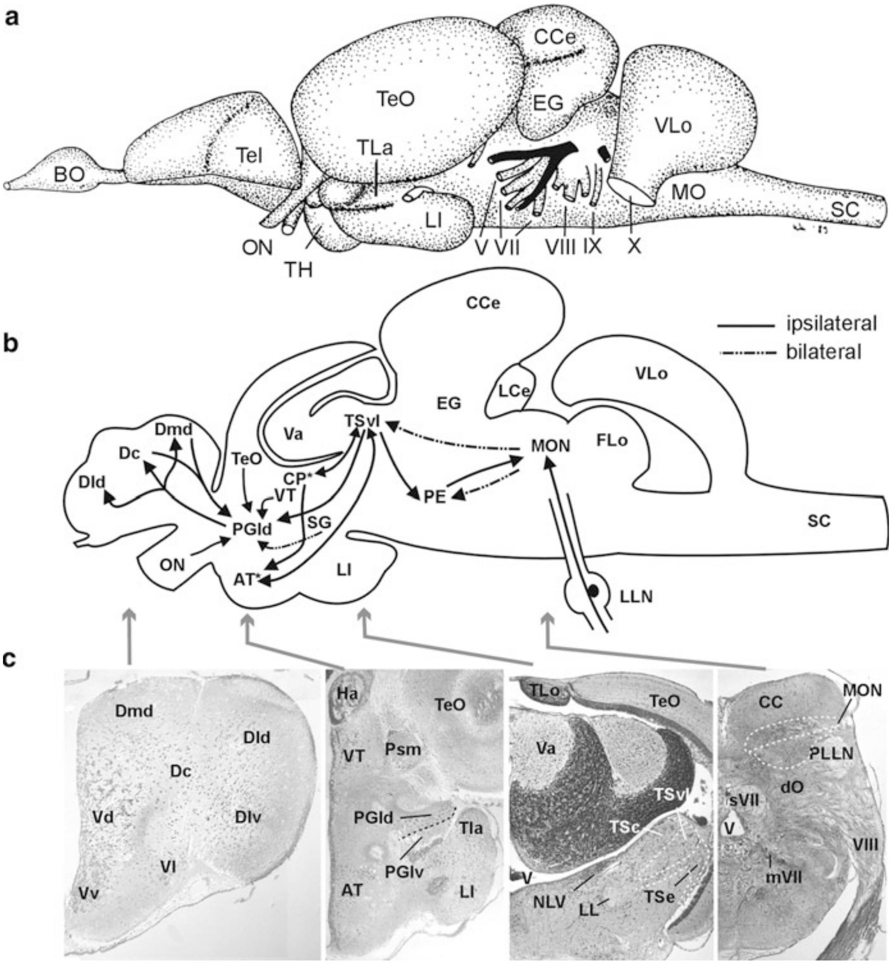

Fig. 6 Lateral line structures and pathways in cyprinids. (**a**) Lateral view of the goldfish (*Carassius auratus*) brain. Lateral line nerves are indicated in black. (**b**) Schematic lateral view of cyprinid brain showing mechanosensory lateral line pathways (for citations see text). * these two (central posterior thalamic and anterior tuberal) auditory nuclei project to the medial pallial zone (Dm; see text). The lateral line nerve (LLN) shown is meant to represent both anterior and posterior nerves. Commissural projections of MON and input from the eminentia granularis to MON are not shown (see text for details). (**c**) Four microphotographs show lateral line mechanosensory structures in transverse sections of goldfish brain stained with Bodian-silver procedure at telencephalic, diencephalic, mesencephalic, and rhombencephalic levels from left to right. Note that the dorsal crest cell area and the deep area of MON are indicated with stippled white lines. Abbrevations: AT anterior tuberal nucleus, BO bulbus olfactorius, CC crista cerebellaris, CCe corpus cerebelli, CP central posterior thalamic nucleus, Dc, Dld, Dlv, Dmd central, dorsolateral, ventrolateral, dosomedial zone of pallial area dorsalis telencephali, dO descending octaval nucleus, EG eminentia granularis, FLo facial lobe, Ha habenula, LCe lobus caudalis cerebelli, LI lobus inferior, LL lateral lemniscus (lateral longitudinal fascicle), LLN lateral line nerves, MO medulla oblongata, MON medial octavolateralis nucleus, mVII facial

cerebellar corpus (Puzdrowski, 1989). The anterior and posterior lateral line fiber terminations are segregated in MON and CON, with ALLN fibers lying anteroventrally and PLLN fibers posterodorsally. Within the eminentia granularis, ALLN fibers terminate anteriorly to those of the PLLN. A small zone of overlap between primary anterior lateral line and octaval nerve projections exists in the dorsal part of the magnocellular and descending octaval nuclei (Puzdrowski, 1989; McCormick & Braford, 1994). As in all gnathostome fishes, the cyprinid MON is covered by the cerebellar crest (Fig. 6c) which contains stellate and other cells. Large crest cells are located in an intermediate region between cerebellar crest and the deeper region of MON. The crest cells have peripheral dendrites extending into the cerebellar crest and either do or do not have basal dendrites into the deeper MON area where mostly granular cells were reported (New et al., 1996). The deeper MON area is recipient of primary lateral line input, whereas the cerebellar crest likely receives parallel fiber input from the eminentia granularis.

Both types of cyprinid MON crest cells give rise to commissural projections (not shown) and to second order lateral line projections ascending in the lateral lemniscus (Fig. 6b). These fibers terminate bilaterally, albeit with a stronger contralateral component, in the ventrolateral nucleus of the torus semicircularis (TSvl) and there are also reciprocal connections with the preeminential nucleus (McCormick & Hernandez, 1996; Fig. 6b). Furthermore, there are weaker projections from MON to the optic tectum and the principal sensory trigeminal nucleus (McCormick & Hernandez, 1996; both not drawn in Fig. 6b). The ventrolateral toral nucleus in turn has strong ipsilateral ascending projections to the dorsal division of the lateral preglomerular nucleus (PGld; Echteler, 1984; McCormick & Hernandez, 1996; Northcutt, 2006). This diencephalic nucleus in turn provides one of the strongest inputs to the dorsal telencephalic (pallial) area in cyprinids, in particular to the dorsal part of the lateral zone (Dld), but also weakly to the dorsal part of the medial zone (Dmd) and to the central zone (Dc) (Striedter, 1992; Northcutt, 2006; Yamamoto & Ito, 2008). Within the dorsolateral preglomerular nucleus (PGld), various sensory inputs are spatially segregated, with (2nd order visual) input from the optic tectum located dorsolaterally, retinal inputs dorsomedially, ventrolateral toral (lateral line) input ventrolaterally, and ventromedial thalamic (likely

Fig. 6 (continued) motor nucleus, NLV nucleus lateralis valvulae, ON optic nerve, PE preeminential nucleus, PGld dorsal part of lateral preglomerular nucleus, PGlv ventral part of lateral preglomerular nucleus, PLLN posterior lateral line nerve, PSm magnocellular superficial pretectal nucleus, SC spinal cord, SG subglomerular nucleus, sVII sensory root of facial nerve, Tel telencephalon, TeO tectum opticum, TH tuberal hypothalamus, TLa torus lateralis, TLo torus longitudinalis, TSc central nucleus of torus semicircularis, TSe external nucleus of torus semicircularis, TSvl ventrolateral nucleus of torus semicircularis, V ventricle, Vd, Vl, Vv dorsal, lateral, ventral nucleus of subpallial area ventralis telencephali, Va valvula cerebelli, VLo vagal lobe, VT ventral thalamus, V trigeminal nerve, VII facial nerve, VIII octaval nerve, IX glossopharyngeal nerve, X vagal nerve somatosensory) inputs ventromedially. In contrast, the ventrolateral preglomerular nucleus (PGlv) receives auditory information from the medial pretoral nucleus (an additional midbrain toral nucleus in ostaryophysines that is postsynaptic to the auditory central toral nucleus; Striedter, 1991, 1992). Both the central posterior thalamic nucleus (the dorsal thalamic auditory "relay" nucleus that receives a main input from the central toral nucleus; Echteler, 1984; Lu & Fay, 1995; Yamamoto & Ito, 2005) and the hypothalamic anterior tuberal nucleus (a second diencephalic auditory target of the auditory central toral nucleus) have reciprocal connections with the (lateral line related) ventrolateral toral nucleus and project in turn to the medial (Dm), but not to the lateral pallial zone (Dl) (Northcutt, 2006). The dorsolateral preglomerular nucleus receives additional input from the subglomerular nucleus (Yamamoto & Ito, 2008). The central posterior thalamic nucleus (CP) also projects to the anterior tuberal nucleus (AT; Fig. 6; Striedter, 1991; Northcutt, 2006), but apparently not to PGld (Yamamoto & Ito, 2008). Thus, all these diencephalic nuclei may be involved in lateral line forebrain circuitry (Fig. 6b).

The descending connections within the cyprinid central lateral line mechanosensory system start out with the medial and central pallial zones projecting back onto the lateral preglomerular nucleus (Striedter, 1992; Northcutt, 2006; Yamamoto & Ito, 2008). However, there are no descending projections from the lateral preglomerular nucleus to the ventrolateral toral nucleus (Striedter, 1992). The ventrolateral toral nucleus projects in turn via a brain stem nucleus, the preeminential nucleus, to the primary sensory MON (McCormick & Hernandez, 1996). Finally, as in most teleosts investigated, the cyprinid mechanosensory system has two separate efferent octavolateralis neuronal populations in the region anterior to the visceromotor column and a third one in the diencephalic periventricular area of the posterior tuberculum, the latter seems special for cyprinids (Zottoli & van Horne, 1983; Puzdrowski, 1989). Thus, while the teleostean lateral line mechanosensory and octaval nerves do not have true somatomotor nuclei whose axons contact motor endplates of muscle fibers, they do have efferent cholinergic octavolateralis neurons that innervate their peripheral sensory organs (Danielson et al., 1988; Roberts & Meredith, 1989, 1992).

Results from neurophysiological studies on the peripheral (Fukuda, 1974; Chapter by Chagnaud & Coombs) and central (Bleckmann 2008; Chapter by Bleckmann & Mogdans) nervous system in cyprinids (and other teleosts) are consistent with the view that the lateral line neuronal network (outlined in Fig. 6b) detects and processes hydrodynamic stimuli which indicate relative movement between water and animal at low frequencies (up to 200 Hz) over relatively short distances (1 to 2 body lengths) to the fish (Mogdans et al., 1997; Mogdans & Kröther, 2001; Künzel et al., 2011; Chapter by Montgomery, Coombs & Bleckmann). This general information is relayed to the MON via lateral line fibers that encode for two submodalities. Lateral line fibers that innervate superficial neuromasts deal with low frequency stimuli (related to velocity/displacement) and appear to play a role in rheotaxis (orientation to water currents; Montgomery et al., 1997). In contrast, fibers innervating canal neuromasts (related to acceleration) detect higher frequency hydrodynamic stimuli and appear to play a role in sensing and localizing discrete hydrodynamic sources, such as prey or predators – especially in the presence of background water flow noise (Engelmann et al., 2000; Kröther et al., 2002; Chapters by Montgomery, Coombs & Bleckmann; Chagnaud & Coombs). Physiological evidence further indicates that ventrolateral toral nucleus units at midbrain levels maintain the functional separation of these two submodalities.

In addition, the ventrolateral torus appears to preserve the anteroposterior topography of external moving objects (Wojtenek et al., 1998; Plachta et al., 2003; Engelmann & Bleckmann, 2004). However, it remains unclear if and where spatial maps based on lateral line information are present in the midbrain (Voges & Bleckmann, 2011).

The representation of mechanosensory lateral line stimuli in the cyprinid diencephalon remains unclear. After visual, acoustic or hydrodynamic stimulation, recordings in the goldfish diencephalon revealed multimodal unit responses in the anterior tuberal nucleus (AT) and unimodal ones (including lateral line stimuli) in the central posterior thalamic nucleus (CP; compare Fig. 6b; Kirsch et al., 2002). However, this study did not find evoked potential or unit responses after acoustic or lateral line stimulation in the lateral preglomerular nucleus. Knowing now the small extent of the lateral line input within the multisensory dorsolateral preglomerular nucleus (Northcutt, 2006; Yamamoto & Ito, 2008; see discussion above), this area might simply have been missed. Unfortunately, there are no physiological recordings in the cyprinid telencephalon related to hydrodynamic stimulation.

Finally, non-electrosensory teleosts other than cyprinids shall be considered. In elopomorph (European eel; Meredith et al., 1987), salmonid (rainbow trout; Schellart et al., 1992) and various acanthomorph teleosts (pike cichlid: McCormick, 1983; oscar: Meredith, 1984; O’Marra & McCormick, 1999; toadfish: Highstein et al., 1992; sleeper goby: Tomchick & Lu, 2005; damselfish: Maruska & Tricas, 2009) a similar picture has emerged regarding primary lateral line nerve projections to MON and CON, as well as to the granular eminence. Except for the trout, all investigated species receive such input to the dorsal part of the magnocellular octaval nucleus, with the oscar also receiving input to the dorsal part of the descending octaval nucleus. In a scorpaenid teleost, an ascending synaptic chain of connections has been reported from MON via the semicircular torus to a preglomerular nucleus and to a thalamic “ventromedial nucleus” (likely corresponding to the central posterior thalamic nucleus, see above); the latter two diencephalic lateral line targets in turn project to various dorsal pallial areas (Murakami et al., 1986). However, auditory and lateral line mechanosensory components have not been resolved anatomically, let alone physiologically, in this study. In the plainfin midshipman, ascending lateral line connections from MON via the midbrain ventrolateral torus (TSvl) reach the diencephalic posterior thalamic nucleus. However, midbrain projections to other diencephalic nuclei (e.g., the lateral preglomerular, central posterior thalamic and anterior tuberal nuclei) have not been demonstrated in this species, nor have descending projections from the midbrain (TSvl) via 2nd order (preeminential nucleus) to 1st order (MON) hindbrain lateral line nuclei (Weeg & Bass, 2000).

Clupeiform fishes (e.g., herrings) represent a special case. Their swim bladder forms paired anterior diverticulae (auditory bullae) which are in close physical contact both with the utricle and cephalic lateral line canals. Sound pressure waves, thus, act on both hair cell systems. Centrally then, a large unique utricular projection area - fused in the midline - is present in the dorsomedial descending octaval nucleus which receives at the same time an extraordinarily extensive overlapping projection from the lateral line nerves (Meredith, 1985; McCormick, 1997), seemingly an adaptation to the peripheral specialization. Naturally, primary lateral line projections in clupeiforms also reach the MON/CON and the eminentia granularis.

A comparison of mechanosensory lateral line central neuroanatomy in ostaryophysines, other non-electrosensory teleosts and basal ray-finned fishes (see Section 4.1) indicates that the situation in cyprinids represents much of the ancestral evolutionary condition for teleosts. This applies in particular to the synaptic hierarchical chain of ascending lateral line connections from (1) the hindbrain MON, to (2) the ventrolateral toral nucleus in the midbrain, to (3) the dorsolateral preglomerular nucleus in the diencephalon to, finally, (4) the telencephalic pallium, as these connections have been found in other ray-finned fishes as well.

In contrast, specialized derived characters are seen in the lateral line nerve projections to the cerebellum. While such projections to the eminentia granularis are generally present in teleosts, lateral line nerve input to corpus and, in particular, valvula cerebelli is more rarely seen and has evolved several times independently (summarized in Wullimann et al., 1991).

Moreover, cyprinid ascending lateral line pathways were revealed to be more complex than previously known (Fig. 6b). There may be additional lateral line pathways via two predominantly auditory centers, the hypothalamic anterior tuberal nucleus and the central posterior thalamic nucleus (see above). Also, the dorsolateral preglomerular nucleus contains in addition to the small lateral line territory a mosaic of various sensory inputs, such as visual (tectum, retina) and somatosensory (ventral thalamus) inputs. It remains to be shown if and how these modalities are separately maintained at pallial levels. In any case, the dorsolateral (lateral line related) and ventrolateral (auditory related) preglomerular nuclei in the diencephalon have largely separate projection areas within the lateral pallial zone in the telencephalon (Yamamoto & Ito, 2008).

According to developmental (Wullimann, 2009; Mueller & Wullimann, 2009), connectional (Northcutt, 2006; Yamamoto & Ito, 2008) and behavioral data (Rodríguez et al., 2002; Salas et al., 2003), it is now widely accepted that the teleostean lateral pallial zone (Dl) is homologous to the medial pallium (hippocampus), whereas the medial pallial zone (Dm) would correspond to the ventral pallium (pallial amygdala). In this context it is interesting to point out that there is segregation of indirect auditory input from the medial pretoral nucleus via the ventrolateral preglomerular nucleus to the ventrolateral pallial zone (hippocampus homologue) and the more direct auditory input from the central toral nucleus via the anterior and caudolateral preglomerular nuclei to the medial pallial zone (pallial amygdala homologue; Northcutt, 2006).

However, a simplistic interpretation of teleostean pallial functions based on the situation for the respective homologous pallial areas in mammals (i.e. Dl only for spatial memory based on sensory detail and Dm for fear conditioning/emotional processing) may lead astray. In reptiles and birds, the ventral pallium (pallial amygdala homologue/nidopallium), which would appear to be homologous to the teleostean Dm, is greatly enlarged in comparison to mammals and, unexpectedly, concerned with the processing of sensory detail (Bruce and Neary, 1995; Martínez-Garcia et al., 2009). Thus, an independent case of ventral pallial enlargement and functional specialization may have occurred in teleosts and birds/reptiles. The situation for the teleostean Dl (hippocampus homologue) corresponds closely to other anamniotes, as the medial pallium is always the target of diencephalic lateral line projections (see Sections 2; 3). Of note, Wullimann & Mueller (2004) have previously proposed that Dc and those portions of Dl/Dm directly surrounding Dc may be dorsal pallium. However, it appears now that all of Dm (ventral pallium), all of Dl (medial pallium; Northcutt, 2006; Yamamoto & Ito, 2008) and Dc (dorsal pallium; Mueller et al., 2011) might each represent separate major pallial divisions.

4.3 Electrosensory Teleosts

The extensive functional neuroanatomical literature on teleostean electroreception can not be completely summarized here. For example, the finer structure of the primary electrosensory lateral line lobes (ELL) or other central electrosensory structures, and in particular the central electromotor system are reviewed elsewhere (Chapters in Bullock & Heiligenberg, 1986; Bell et al., 1993; Bullock et al., 2005). In line with the present chapter's focus, the ascending central (lateral lemniscal) lateral line pathways in electrosensory teleosts will be discussed.

As noted above, the perception of weak electric fields (electroreception) using multicellular sensory organs (end buds in lampreys and ampullary organs in gnathostomes) innervated by lateral line nerves is ancestral for vertebrates. The signals perceived by ampullary organs with high sensitivity are DC or low frequency electric fields originating from prey, ocean currents, electrochemical sources, or locomotion of the animal in the earth magnetic field (Bodznick & Montogomery, 2005). However, electroreception was lost early in actinopterygian phylogeny (see Section 4.1 and Fig. 1), and re-appeared at least twice, if not four times, within teleosts (Bullock et al., 1982; 1983). Within the osteoglossomorphs, the African mormyrids/gymnarchids and the African knifefishes (i.e., *Xenomystus nigri*) - but not the Asian knifefishes - are electrosensory (Braford, 1986). Among the ostariophysans, both the gymnotoids (South-American knifefishes; Carr & Maler, 1986) and their sistergroup, the silurids (catfishes; Finger, 1986), are electrosensory. Whether xenomystines and silurids acquired electroreception independently of mormyrids and gymnotoids, respectively, is debatable. Although silurids and xenomystines have ampullary organs for passive electroreception, they lack weakly electric organs (except for a unique weakly electric organ dorsal to the swim bladder in synodont catfishes; Hagedorn et al., 1990). In contrast, mormyrids (e.g., elephantnose fish, *Gnathonemus petersii*) and gymnotoids (e.g., chocolate ghost, *Apteronotus leptorhychus; glass knifefish, Eigenmannia virescens*) have active electroreception. A weakly electric organ (usually consisting of modified axial musculature; comprised of motor neurons in apteronotids) in the tail of these two distantly related groups emits low voltage electric signals (electric organ discharges, EODs) which are used in conjunction with specialized electroreceptors for electrolocation and electrocommunication (Bullock & Heiligenberg, 1986; Bell et al., 1993; Bullock et al., 2005). The degree of parallelism is striking. Besides the presence of electric organs, both mormyrids and gymnotoids exhibit three types of electroreceptors. One is specialized for low-frequency (passive) electroreception (ampullary organs, similar to those in other electrosensory teleosts), the other two are dedicated to high-frequency (active) electrolocation and electrocommunication (two types of tuberous organs exclusive for these teleosts).

4.3.1 Silurids

Given the phylogenetic relationship of cyprinids (the outgroup of characins, silurids and gymnotoids) and characins (outgroup of silurids and gymnotoids, the latter two being sister groups), the analysis of representatives from these families offers to reveal the evolutionary history of central nervous octavolateralis pathways in ostaryophysan teleosts. Thus, having already treated the soley mechanosensitive cyprinids, we shall now consider the central nervous lateral line centers in passive electrosensory silurids and active electrosensory gymnotoids.

The catfish rhombencephalic octavolateralis area displays in addition to five primary auditory nuclei (McCormick & Braford, 1993) and the primary mechanosensory MON, a very large, laterally situated electrosensory lateral line lobe (Figs. 7b, b'; ELL; Finger, 1986). Unlike in other electrosensory vertebrates discussed above (Figs. 2, 3), both the anterior and the posterior lateral line nerve ganglia (ALLN and PLLN) give rise to electrosensory fibers in addition to mechanosensory fibers (Fig. 7; Tong & Finger, 1983; Finger & Tong, 1984; Northcutt et al., 2000). The ALLN and PLLN projections are segregrated within the MON, the ELL and the eminentia granularis with the head represented medially and the trunk laterally in each structure. There is some very limited overlap between lateral line and octaval projections in the magnocellular and part of the descending octaval nuclei. Both MON and ELL are covered by a molecular layer (cerebellar crest) which receives tangential fibers originating in granule cells of the eminentia granularis and the caudal cerebellar lobe. However, the primary lateral line nerve fibers terminate in deeper layers of MON and ELL. Lateral lemniscal projections from the catfish MON and ELL arise from crest cells at the boundary between cerebellar crest and deeper layers of MON and ELL. The MON has bilateral projections through the lateral lemniscus to the midbrain ventral toral nucleus

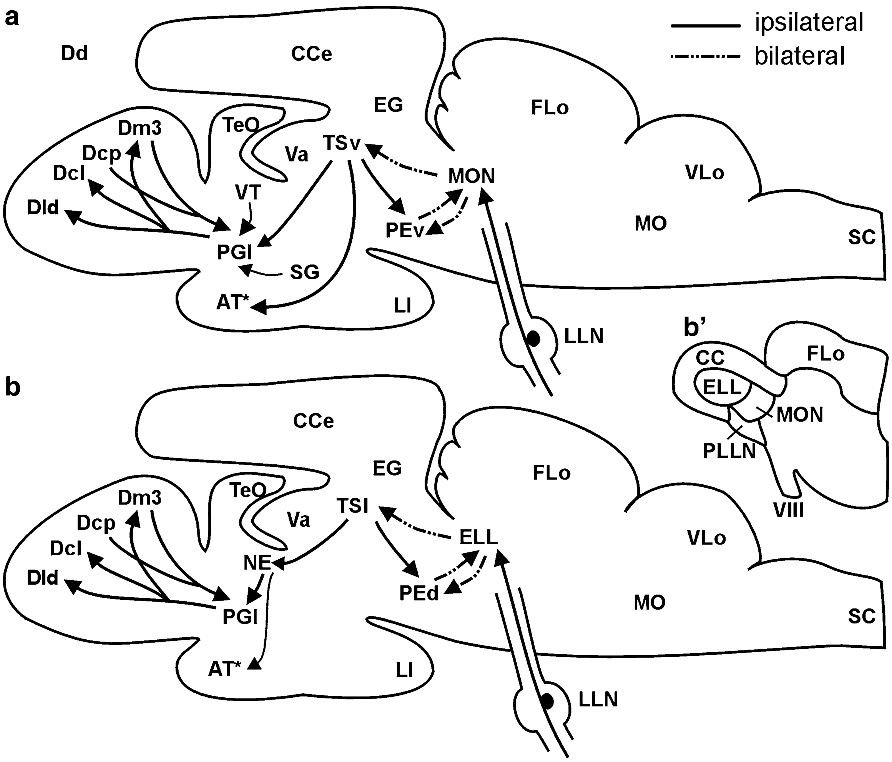

Fig. 7 Lateral line pathways in silurids. Schematic lateral views of catfish brain showing mechanosensory (**a**) and electrosensory (**b**) lateral line pathways (for citations see text). The hypothalamic auditory nucleus marked by an asterisk also receives mechano- (from TSv) and electrosensory (from NE) input and projects to different medial pallial subzones (Dm2/Dm4) than PGl does (see text). The illustrated lateral line nerve (LLN) represents both anterior and posterior nerves. Input from the eminentia granularis and caudal cerebellar lobe to MON and ELL is not shown (see text). (**b'**) is a transverse section through one side of catfish electrosensory lateral line lobe and medial octavolateralis nucleus. Abbrevations: AT anterior tuberal nucleus, CCe corpus cerebelli, Dcl, Dcp, Dld, Dm3 centrolateral, centroposterior, laterodorsal, medial zone 3 of pallial area dorsalis telencephali, EG eminentia granularis, ELL electrosensory lateral line lobe, FLo facial lobe, LI lobus inferior, LLN lateral line nerves, MO medulla oblongata, MON medial octavolateralis nucleus, NE nucleus electrosensorius (pretectum), PEd, PEv dorsal, ventral preeminential nucleus, PGl lateral preglomerular nucleus, PLLN posterior lateral line nerve, SC spinal cord, SG subglomerular nucleus, TeO tectum opticum, TSl, TSv lateral, ventral nucleus of torus semicircularis, Va valvula cerebelli, VT ventral thalamus, VLo vagal lobe, VIII octaval nerve

(TSv), ventral preeminential nucleus and optic tectum (the latter connection not shown in Fig. 7a). The silurid TSv, in turn, projects via the ventral preeminential nucleus back to MON (Finger & Tong, 1984).

Pioneering neuroanatomical and electrophysiological work (Knudsen, 1977; Tong, 1982; Tong & Finger, 1983) established that similar parallel electrosensory pathways to the midbrain exist in catfishes. The silurid torus semicircularis has in addition to the central (TSc; auditory), medial pretoral (MPN; auditory) and ventral (TSv; mechanosensory) nuclei, which are also present in cyprinids, a large lateral toral nucleus (TSl; Knudsen, 1977; Finger, 1986; Striedter, 1991). The TSl receives the bulk of efferents from the ELL and projects via the dorsal preeminential nucleus back to ELL (Fig. 7b). The preeminential fibers enter the cerebellar crest of MON and ELL tangentially. Interestingly, New & He (1998) did not confirm a toral input to the catfish preeminential nucleus, but did report input to it from primary auditory nuclei. Early neuroethological studies also demonstrated that there is a lateral line mechanosensory pathway from TSv via the anterior tuberal nucleus (then interpreted as "thalamic") to the medial pallial zone (Finger, 1980; Finger & Bullock, 1982). Subsequent studies explored the auditory, mechanosensory and electrosensory pathways from midbrain to forebrain in silurids and other ostariophysan teleosts.

The catfish diencephalic lateral preglomerular nucleus receives its major input from the mechanosensory TSv (Striedter, 1992). Only a small ventral division of the catfish PGl receives input from the (auditory) MPN (Striedter, 1992), which is highly reminiscent of dorsal (multisensory) and ventral (auditory) PGl divisions in cyprinids (see Section 4.2). Also similar to cyprinids, PGl receives minor inputs from the ventral thalamus and subglomerular nucleus; however, tectal and retinal inputs to PGl have not been reported for catfish (Striedter, 1990). An additional dense input to the catfish PGl arises from the pretectal nucleus electrosensorius (NE; Fig. 7b; see below). Since a weak input from the central pretectal nucleus to PGl is also seen in goldfish (Striedter, 1992; although not confirmed by Yamamoto & Ito, 2008), NE might have evolved from a pretectal cell population that separated from the central pretectal nucleus in silurids (and gymnotoids). As seen in cyprinids, the silurid central posterior thalamic (CP) and anterior tuberal nuclei (AT) are targets of both the auditory TSc and MPN in the midbrain. The mechanosensory TSv additionally projects to AT in the catfish (Finger, 1986; Striedter, 1991), but an input of TSv to the catfish CP has not been reported. The AT in turn interconnects reciprocally with pallial zones Dm2 and Dm4, which are distinct from the PGl projection zones (Striedter, 1991). The latter are in the medial, central and lateral pallial zones (Dm3, Dcl, Dld), and projections back to PGl arise from the central (Dcp) and medial divisions (Dm3) (Striedter, 1991). Since doubts have been raised about whether the dorsal pallial division (Dd) is really a separate pallial division (Mueller et al., 2011), Dd is assumed here to be part of Dm.

Silurid electrosensory pathways run from the TSl to the (pretectal) nucleus electrosensorius, which then, via the PGl, reach the pallium (Dm3, Dcl, Dld). The NE also projects weakly to the anterior tuberal nucleus (AT; Striedter, 1991) indicating that auditory, mechanosensory and electrosensory information is processed there. Also at the level of the diencephalic PGl and telencephalic pallial zones, the mechanosensory and electrosensory pathways appear to converge (Fig. 7). Thus, it is not clear whether and how parallel processing is maintained between lateral line electro- and mechanosense (and audition) in the forebrain of catfishes.

4.3.2 Gymnotoids

The sistergroup of silurids, the weakly electric gymnotoids, possess in their skin from head to tail not only mechanosensory neuromasts and electrosensory ampullary organs, but also two types of electrosensory tuberous organs, called T-units (phase coders, which fire in synchrony with the EOD) and P-units (probality coders, which reflect EOD amplitude modulations in their discharge probability) (Heiligenberg, 1984; Carr & Maler, 1986; Bell & Maler, 2005). Only information on wave-type gymnotoids (which emit continuous EODs at highly regular, but individual, frequencies) will be discussed here, since far less is known on pulse-type species (which emit pulse-like EODs). Unlike in catfish, the peripheral electrosensory lateral line fibers in gymnotoids originate exclusively in the anterior lateral line nerve ganglia (with a recurrent lateral line ramus innervating the body trunk); the central fibers terminate in a gigantic electrosensory lateral line lobe (ELL, Figs. 8b, b”). The mechanosensory fibers from both ALLN and PLLN project topographically to the small MON (Fig. 8a; Maler et al., 1974; Vischer et al., 1989; Lannoo et al., 1989). Historically, the ELL and MON were named posterior and anterior lateral line lobe, respectively. Primary electrosensory fibers enter the deep neuropil layer of ELL, with T-unit fibers synapsing (electrotonically) on spherical cell bodies and P-unit fibers terminating (with chemical synapses) on basal dendrites of basilar pyramidal cells (E-cells which are excited by a rise in EOD amplitude) and, via (inhibitory) granular interneurons, on nonbasilar pyramidal cells (I-cells which are excited by a fall in EOD amplitude) (Heiligenberg, 1986; Bell & Maler, 2005). The medial segment of the ELL, where ampullary organ fibers terminate (see below), does not contain spherical cells (Maler, 1979). Cell bodies of basilar and nonbasilar pyramidal cells lie between molecular and deeper ELL layers (comparable to crest cells, see Sections 3; 4.2). Additional primary lateral line nerve projections reach the eminentia granularis, which, in turn, projects back to the contralateral superficial molecular layer of the ELL (Maler et al., 1974; Bell & Maler, 2005).

Neuroanatomical and electrophysiological studies revealed that the gymnotoid ELL exhibits four complete maps of the electrosensory body surface in medial, centromedial, centrolateral and lateral segments (Fig. 8b, b”), with the medial one receiving ampullary organ information and the remaining three segments receiving tuberous organ information (Heiligenberg & Dye, 1982; Carr & Maler, 1986; Lannoo et al., 1989). Thus, each electrosensory fiber that innervates a tuberous organ terminates in all three maps on pyramidal or spherical cells with varying degrees of convergence dependent on peripheral receptor density (the head is consistently overrepresented). The maps differ in size and, thus, in spatial resolution (Carr et al., 1982; Shumway, 1989). Furthermore, centromedial map lesions lead to deficits in the jamming avoidance response (JAR, see below), whereas lateral map lesions impair electrocommunication responses (Metzner & Juranek, 1997). While the head is always represented in the same orientation in each map, the dorsoventral axis is inverted in centromedial and lateral segments compared to the other two segments (v for ventral in Fig. 8b).

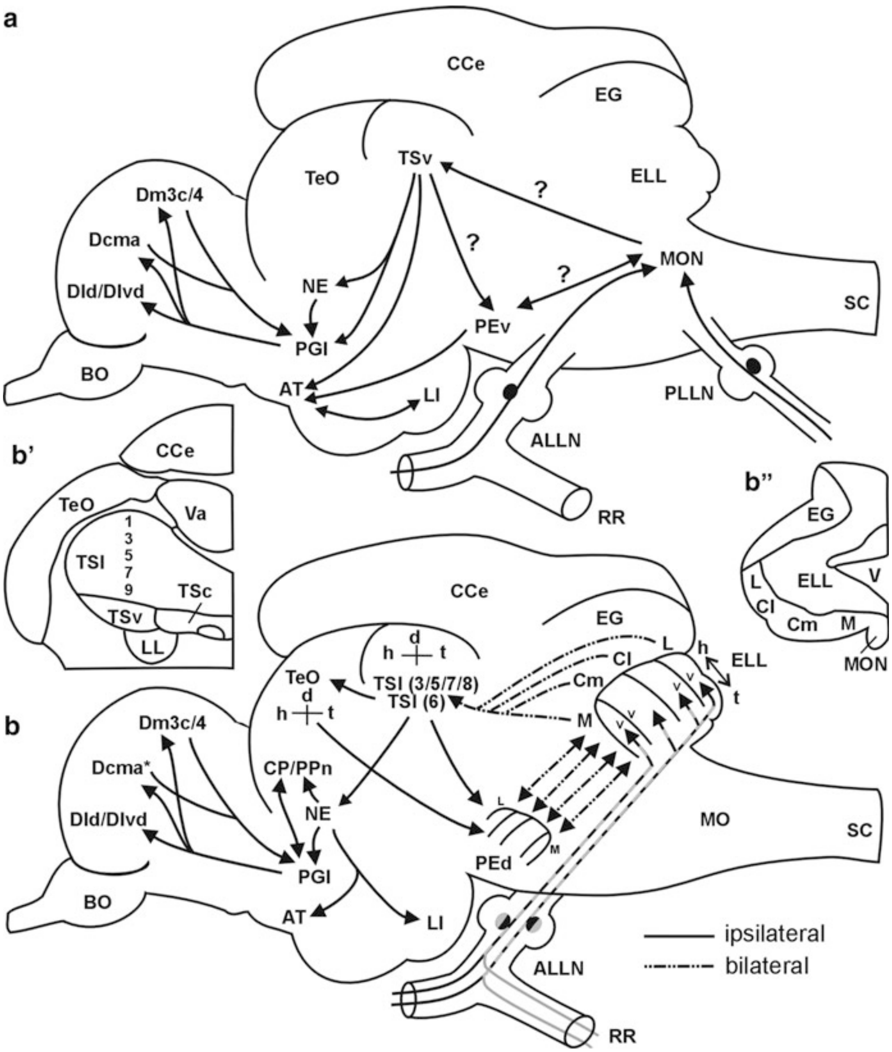

Fig. 8 Lateral line pathways in gymnotoids. Schematic lateral views of South-American knifefish brain showing (**a**) mechanosensory and (**b**) electrosensory lateral line pathways (for citations see text). Note that each of the four segments of electrosensory lateral line lobe and preeminential nucleus contains a map of the fish's entire electrosensory body surface (h: head, t: tail) with alternating dorsoventral orientation (v: ventral). ELL maps are shown as they appear in dorsal view on the right side of the body, whereas PEd maps are shown for the left body side. (**b**') is a transverse section through one side of the midbrain showing toral divisions. (**b**") is a transverse section through one side of ELL-EG, showing the arrangement of segments. Ampullary organs are represented in the medial segment and tuberous organs in the remaining segments. The lateral torus semicircularis and optic tectum each display a single, merged electrosensory map. *The central pallial zone (Dcma) projects to optic tectum and lateral torus semicircularis (not drawn, see text). Abbrevations: ALLN anterior lateral line nerve, AT anterior tuberal nucleus, BO bulbus

Pyramidal and spherical cells are the efferent cells of the ELL. They project bilaterally (mostly contralaterally) to the lateral torus semicircularis (TSl, also called TSd). Pyramidal cells (representing P-unit and ampullary organ information) also give off collaterals to the dorsal preeminential nucleus (PEd; Carr et al., 1981; Scheich & Ebbesson, 1981; Maler et al., 1982). Topographical information from several body maps (P-units, ampullary organ, but not T-units) is maintained in the efferent projections to the dorsal preeminential nucleus (Maler et al., 1982; Sas and Maler, 1983) and the maps are, thus, processed there in parallel (Fig. 8b). In contrast, the four ELL maps converge to a single map in the lateral torus semicircularis, with different electroreceptor type information segregated into different layers (Figs. 8b, b'; T-types in layer 6, P-types in layers 3/5/7/8, ampullary organs in 3 and 7; Carr et al., 1981; Rose & Heiligenberg, 1985; Carr & Maler, 1986; Carr et al., 1986). However, layer 6 neurons extend axons into layer 5/7 and also dendrites into adjacent layers. Thus, layer 6 neurons may receive information from and influence neurons dealing with P-type signals, indicating a first interaction of T- and P-systems. Both diffuse inhibitory and topographic excitatory (reciprocal) projections arise from the dorsal preeminential nucleus and terminate in the ELL. That is, inhibitory bipolar cells terminate on pyramidal cell bodies, while excitatory stellate cells synapse in the lower molecular layer of the ELL on pyramidal cell apical dendrites. Granular cells of the eminentia granularis also terminate in the ELL (upper molecular layer contralaterally/ventral molecular layer ipsilaterally), whereas eurydendroid cells (the teleostean homologous cells of efferent deep cerebellar nuclei) of the eminentia granularis project contralaterally to the TSl. The PEd furthermore connects reciprocally to the eminentia granularis (EG) bilaterally (connections with the latter not shown in Figure 8b; Sas & Maler, 1987; Bell & Maler, 2005). The TSl projects heavily back to the preeminential nucleus (topography unresolved). This descending TSd-PEd-EG pathway provides the ELL with electrosensory and proprioceptive feedback that helps to maintain sensitivity (gain control) in ELL. The topographical reciprocal connections between PEd and ELL may function as an attentional "searchlight" (Bastian, 1986a, b; Heiligenberg, 1990; Bell & Maler, 2005).

Fig. 8 (continued) olfactorius, Cl, Cm centrolateral, centromedial segment of ELL (tuberous organs), CCe corpus cerebelli, CP/PPn central posterior thalamic/prepacemaker nucleus, d dorsal, Dcma anterior part of centromedial zone of pallial area dorsalis telencephali, Dld, Dlvd, laterodorsal, dorsal part of lateroventral zone of pallial area dorsalis telencephali, Dm3c/4 two divisions of medial zone of pallial area dorsalis telencephali , EG eminentia granularis, ELL electrosensory lateral line lobe, h head, L lateral ELL segment (tuberous organs), LI lobus inferior, LL lateral lemniscus (lateral longitudinal fascicle), M medial ELL segment (ampullary organs), MO medulla oblongata, MON medial octavolateralis nucleus, NE nucleus electrosensorius (pretectum), PEd, PEv dorsal, ventral preeminential nucleus, PGl lateral preglomerular nucleus, PLLN posterior lateral line nerve, RR recurrent ramus of ALLN, SC spinal cord, t tail, TeO tectum opticum, TSc, TSl, TSv central, lateral, ventral nucleus of torus semicircularis, v ventral, V fourth ventricle, Va valvula cerebelli

The gymnotoid TSl also projects ipsilaterally and topographically to central layers of the optic tectum (Sas & Maler, 1986a, b; Heiligenberg & Rose, 1987; Carr & Maler, 1986). Retinal input to the tectum is located more superficially and is in register with electrosensory input (Bastian, 1982; Heiligenberg & Bastian, 1984). The optic tectum also feeds back into the PEd and has descending connections, via the brain stem reticular formation, to the spinal cord (not shown; Behrend & Donicht, 1990). The usual role of the optic tectum is object localization and control of orienting behaviors towards objects of interest (Stein and Rowland, 2011).

Further, the TSl – but not the optic tectum (Keller et al., 1990) - projects to a nucleus dorsal to the preglomerular nucleus, the pretectal nucleus electrosensorius (NE; Carr et al., 1981), probably without maintaining topography. The NE is a complex of four neuronal subpopulations and has a particularly important role in the jamming avoidance response (JAR) through its output to the prepacemaker nucleus (Keller et al., 1990; Bell & Maler, 2005). Through the JAR wave-type species move their EOD frequency slightly away from the frequency of conspecific EODs to minimize signal interference (Heiligenberg, 1986). One subpopulation of NE that processes electrosensory and one that processes acoustic/mechanosensory information also project to the hypothalamic anterior tuberal nucleus and inferior lobe (Keller et al., 1990).

There is controversy whether NE in gymnotoids also projects to the lateral preglomerular nucleus. This connection was found by Striedter in chocolate ghosts (*Apteronotus leptorhynchus*; Striedter; 1992), similar to the situation in silurids (see Section 4.3). Also retrograde tracing from the inferior lobe yielded no retrograde cells in the silurid NE (Striedter, 1991). However, the latter were seen in another gymnotoid (glass knifefish; *Eigenmannia virescens*; Keller et al., 1990) and, thus, NE efferents to the PGl were seen as misinterpreted interrupted fibers to the hypothalamic inferior lobe.

Because there are no direct telencephalic projections from NE (Keller et al., 1990; Wong, 1997), one may wonder how electrosensory information would reach the telencephalon in gymnotoids, if not through PGl, as the anterior tuberal nucleus has no pallial projections in gymnotoids (Giassi et al., 2007), unlike in silurids and cyprinids (see Sections 4.2; 4.3.1). Various gymnotoid pallial areas clearly take part in higher order memory processes related to recognition of conspecifics and are dependent on electrocommunication signals (Harvey-Girard et al. 2010). In any case, the gymnotoid PGl has heavy projections to the telencephalic pallium (Fig. 8b; Striedter, 1992; Zupanc, 1997; Corrêa et al., 1998). Interestingly, the central pallial zone not only projects to the optic tectum, but also to the TSl (not drawn; Corrêa et al., 1998).

The mechanosensory lateral line fibers coming from ALLN (head) and PLLN (trunk; Fig. 8a) terminate separately in MON and eminentia granularis (Maler et al., 1974). Unfortunately, the connections of the gymnotoid MON have not been investigated. However, gymnotoids possess a ventral preeminential nucleus (Sas & Maler, 1983) as do silurids, and a mechansensory division of the torus semicircularis (TSv; Matsubara et al., 1981; Scheich & Ebbesson, 1981; Carr & Maler, 1985). The TSv projects to PGl (Striedter, 1992), to the anterior tuberal nucleus (Giassi et al., 2007) and to a division of the NE (Keller et al., 1990; see above). The anterior tuberal nucleus also receives input from the mechanosensory ventral preeminential nucleus and the hypothalamic inferior lobe (Giassi et al., 2007). Because of the convergences of mechanosensory and electrosensory input to PGl, their relative components within the ascending projections of PGl to the telencephalic pallium can not be discriminated from one another, similar to the situation in silurids.

4.3.3 Mormyrids

Finally, regarding the African mormyriforms, the focus will be on pulse-type EOD emitting mormyrids which are the majority of species - except for the wave-type EOD emitting Aba (*Gymnarchus niloticus*), the only gymnarchid. Like gymnotoids, mormyrids have mechanoreceptive neuromasts, ampullary organs, and two types of tuberous organs (knollenorgans, mormyromasts). However, mormyrid primary lateral line mechanosensory and electrosensory fibers are present in both anterior and posterior nerve ganglia (Fig. 9; Maler et al., 1973a, b; Bell & Russell, 1978; Bell, 1981a). Contrary to most other teleosts, octaval and lateral line nerves both project strongly to the medial octavolateralis nucleus (MON/anterior lobe of Bell, 1981a) and to the anterior octaval nucleus, but with limited overlap within these nuclei; additional minor overlapping projections are seen in the descending octaval nucleus and the eminentia granularis (Bell, 1981a). Therefore, the medial (auditory) part of the mormyrid MON has been interpreted as part of the descending octaval nucleus (McCormick (1992, 1999). Electrosensory fibers terminate in the ELL (posterior lobe of Bell, 1981a) which consists of a cortex and a nucleus of the ELL (Figs. 9c, d; 10a). Surprisingly, there is a small contingent of contralateral primary projections to both MON and ELL (only to cortex; Bell, 1981a).

The mormyrid ELL cortex consists of three zones, each with a somatotopic map of the electrosensory body periphery (note inversion of dorsoventral axis in two lateral zones compared to medial zone; Figs. 9c; 10a). Ampullary organs are represented in the ventrolateral zone and mormyromasts (tuberous receptors for active electrolocation) in the medial and dorsolateral zones (Bell & Russell, 1978; Bell & Szabo, 1986). Mormyromasts contain two sensory cell types, whereby A-type cells project through their innervating fibers to the medial ELL zone (concerned with resistive, dead objects), and B-type fibers project to the dorsolateral zone (concerned with capacitive, living objects; Bell et al., 1989; von der Emde, 1998). A critical difference to gymnotoids is that the fibers innervating the second tuberous receptor type, the knollenorgans (electrocommunication), project (electrotonically) to a separate structure within the ELL, but outside of the cortex, the nucleus of the ELL, which is located medially to the ventrolateral cortical zone (Fig. 10a). Its ascending connections are largely kept in parallel to those of the mormyromast/ampullary organ pathway at least up to the torus semicircularis (unlike in gymnotoids, where P and T-type information converges onto certain TSl cells; see Section 4.3.2).

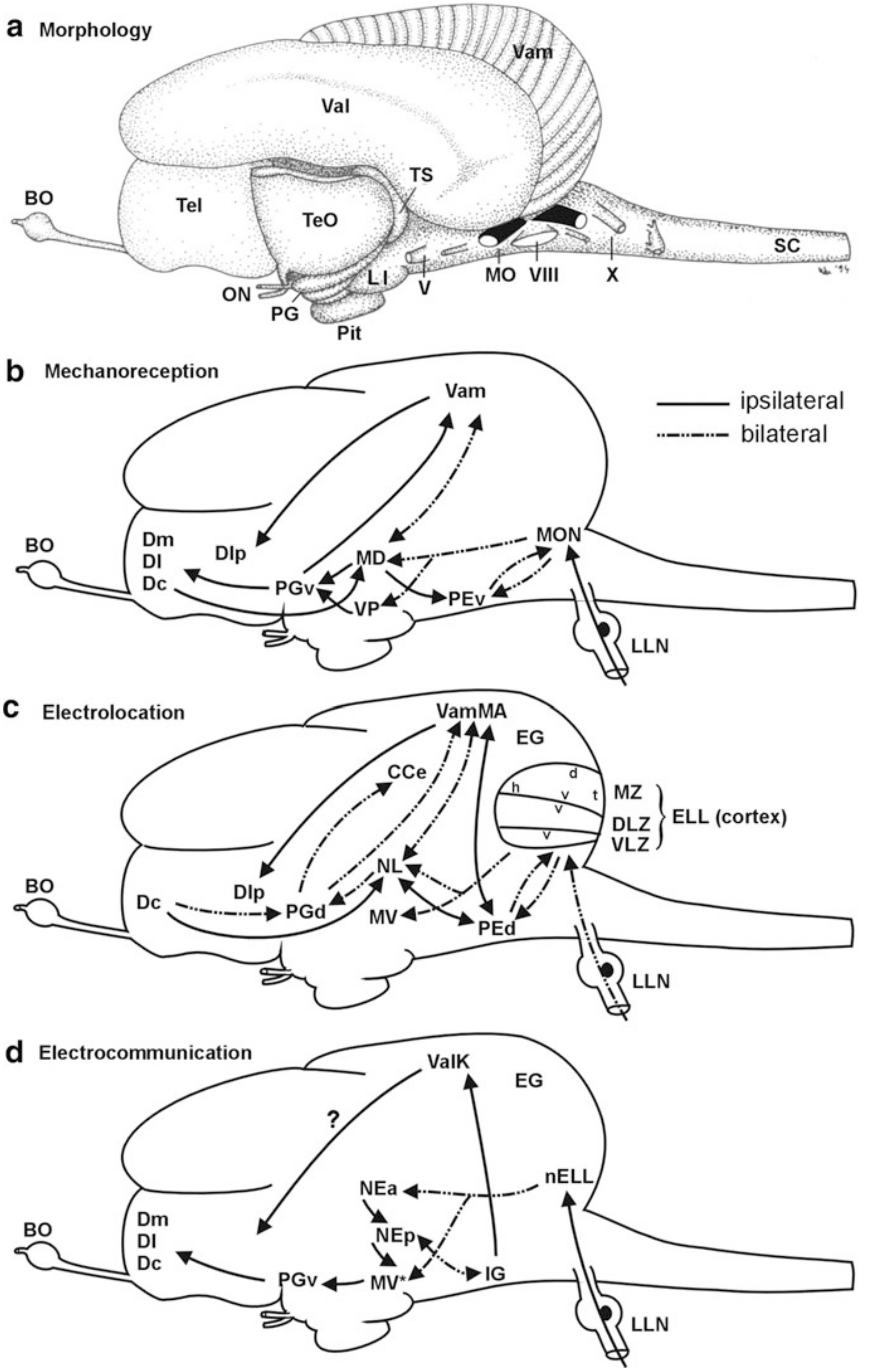

Fig. 9 Lateral line pathways in mormyrid fishes. (**a**) Lateral view of the mormyrid brain (*Gnathonemus petersii*; elephantnose fish). Anterior and posterior lateral line nerves are indicated

The circuitry within the mormyrid ELL is even more complex than in gymnotoids, but nevertheless similar in that it receives eminentia granularis (granular cell) input in its upper level of the superficial molecular layer and (dorsal) nucleus preeminentialis input more deeply. A ganglionic cell layer (Fig. 10a) follows more basally and includes one of the excitatory efferent ELL cell types, the large ganglionic (I- cells: inhibited by stimulation). The second efferent - large fusiform - cell type (E-cells: excited by stimulation) lies in the even deeper granular layer. Here, also granular cells (inhibitory and excitatory ones) are located. They are the exclusive recipients of primary afferent nerve fibers, which enter the ELL basally. The granular cells, in turn, synapse on the two efferent ELL cell types, but also involve loops via (inhibitory) medium ganglionic cells (again E-cells and I-cells) to the efferent cells (Grant et al., 1996; Meek et al., 1999; Bell & Maler, 2005).

The ascending mormyromast/ampullary organ (electrolocation) pathways (Fig. 9c) will now be considered. The mormyrid torus semicircularis contains five nuclei: a large lateral, and somewhat smaller exterolateral, mediodorsal, medioventral, and ventroposterior nuclei (Figs. 10 c-d). In addition to intrinsic commissural (intrazonal) and ispilateral interzonal (between MZ/DLZ) connections (not shown in Fig. 9), the ELL cortex has bilateral efferent projections to the lateral toral nucleus (NL), with collaterals to the medioventral toral nucleus (MV), as well as to the dorsal preeminential nucleus (PEd; Fig. 10b; Bell et al., 1981; Bell & Szabo, 1986; Grant et al., 1996). The heavy projection to NL and PEd is topographical. The three ELL cortical maps of mormyrids converge to one map in PEd (unlike in gymnotoids) and NL (as in gymnotoids). The ELL maps receive topographical reciprocal inputs from PEd medium sized core cells to the deep molecular layer, while small peripheral PEd cells project to the eminentia granularis, which in turn

Fig. 9 (continued) in black. The lateral line nerve (LLN) shown in (**b**) to (**c**) is meant to represent both nerves. Schematic lateral views of mormyrid brain showing (**b**) mechanosensory lateral line pathways, (**c**) mormyromast-ampullary organ electrosensory lateral line pathways (note that each of the three ELL zones contains a complete body map of the electrosensory skin periphery, with differing dorsoventral axes as indicated. Ampullary organs are represented in the ventrolateral zone and mormyromast A-type fibers in medial, and B-type fibers in dorsolateral zone), (**d**) knollenorgan electrosensory lateral line pathways (*MV also projects to ValK). For citations see text. Abbrevations: BO bulbus olfactorius, CCe corpus cerebelli, d dorsal, Dc, Dl, Dlp, Dm, central, lateral, lateroposterior, medial zone of pallial area dorsalis telencephali, DLZ dorsolateral zone of ELL, EG eminentia granularis, ELL electrosensory lateral line lobe, h head, LI lobus inferior, LLN lateral line nerves, MD mediodorsal nucleus of torus semicircularis, MO medulla oblongata, MON medial octavolateralis nucleus, MV medioventral nucleus of torus semicircularis, MZ medial zone of ELL, NEa, NEp anterior, posterior exterolateral nucleus of torus semicircularis, nELL nucleus of the ELL, NL lateral nucleus of torus semicircularis, ON optic nerve, PEd, PEv dorsal, ventral preeminential nucleus, PG preglomerular complex, PGd, PGv dorsal, ventral parts of preglomerular nucleus, Pit pituitary, SC spinal cord, t tail, Tel telencephalon, TeO tectum opticum, TS torus semicircularis, v ventral, ValK lateral leaf of valvula cerebelli (knollenorgan region), VamMA medial leaf of valvula cerebelli (mormyromast/ampullary region), VLZ ventrolateral, zone of ELL, VP ventroposterior nucleus of torus semicircularis, V trigeminal nerve, VIII octaval nerve, X vagal nerve

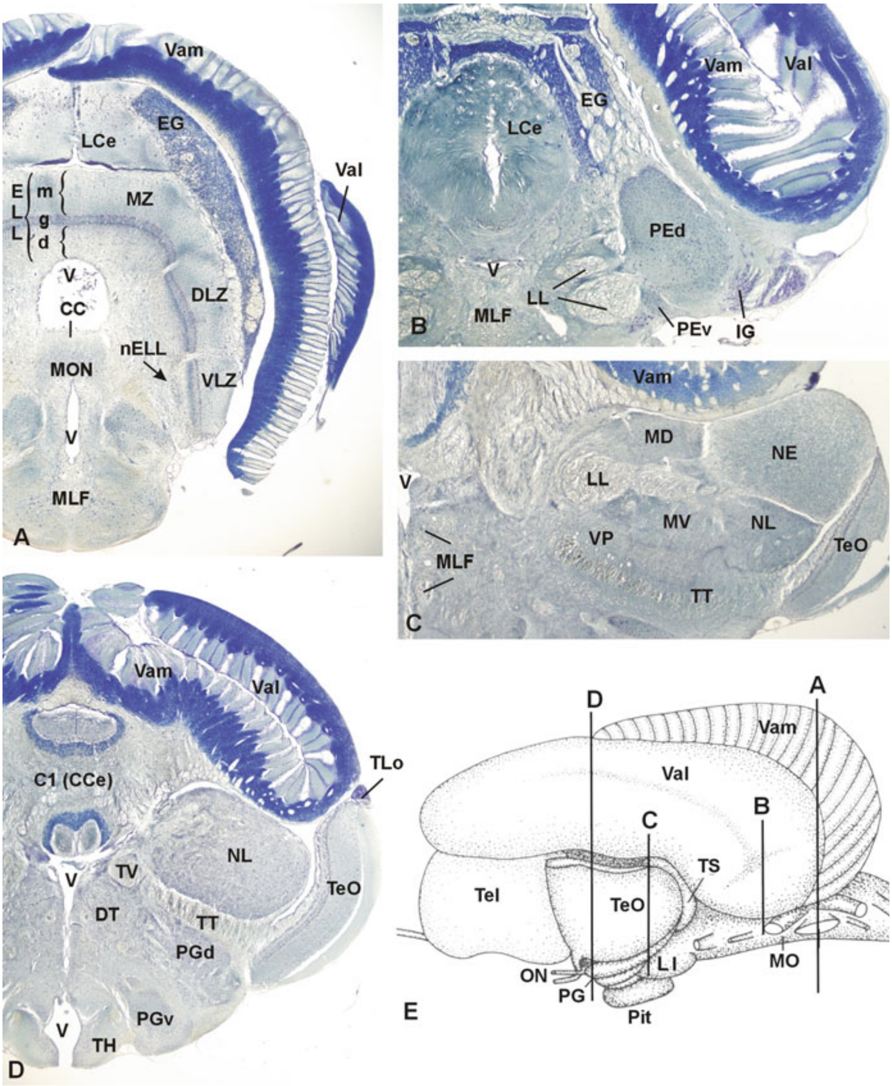

Fig. 10 Electrosensory and mechanosensory lateral line central nervous structures in a mormyrid fish, *Gnathonemus petersii*. Tranverse sections through (**a**) Electrosensory lateral line lobe (ELL) and mechanosensory medial octavolateralis nucleus (MON). Note dome-like structure of ELL below eminentia granularis/caudal cerebellar lobe and valvula cerebelli, as well as breaks between ELL cortex zones. (**b**) preeminential nucleus, (**c**) posterior level of torus semicircularis with all five toral nuclei. (**d**) anterior toral level showing diencephalic preglomerular complex and lateral toral nucleus (electrolocation). (**e**) Drawing of brain with section levels indicated. For citations see text. Abbrevations: CC crista cerebellaris, CCe corpus cerebelli, C1 lobe C1 of CCe, DLZ dorsolateral zone of ELL, d deep layers of ELL, DT dorsal thalamus, EG eminentia granularis, ELL electrosensory lateral line lobe, g ganglionic layer of ELL, IG isthmic granular population, LCe lobus caudalis cerebelli, LI lobus inferior, LL lateral lemniscus (lateral longitudinal fascicle), m molecular layer of ELL, MD, medial nucleus of torus semicircularis, MLF medial longitudinal

projects to the upper molecular ELL layer. The lateral toral nucleus is furthermore reciprocally and topographically connected with PEd (stronger input from PEd than output to PEd) and also has commissural projections (Finger et al., 1981; Bell & Szabo, 1986). The PEd, furthermore, acts - as in gymnotoids - via the eminentia granularis back on the ELL cortex (von der Emde & Bell, 1996; Meek et al., 1999) providing recurrent electrosensory feedback. Another such feedback circuit (similarly present in gymnotoids) runs from eminentia granularis (granular cells) via Purkinje and eurydendroid cells of the caudal cerebellar lobe to PEd and NL (Bell & Maler, 2005; Campbell et al., 2007; circuits involving the eminentia granularis and caudal cerebellar lobe are not shown in Fig. 9).

The NL also projects topographically to the optic tectum (not further considered) and to the diencephalon (dorsal preglomerular nucleus; PGd; Fig. 10d). Comparative considerations allowed for recognition of the preglomerular complex in mormyrids (Wullimann & Northcutt; 1990). Thus, the terms caudal, ventral, and dorsal preglomerular nuclei were introduced to replace formerly used names (posteroventral thalamic, anterior thalamic, and dorsal anterior pretectal nuclei, respectively) which is meanwhile widely accepted (von der Emde & Prechtl, 1999; Meek et al., 1999; Bell & Maler, 2005). Surprisingly however, the PGd does not project to the telencephalon as expected, but rather only receives an input from the central pallial zone (Dc; Wullimann & Northcutt, 1990). The PGd connects instead reciprocally with a particular area in the medial valvula cerebelli, as does the NL (with the valvula projecting additionally to PEd; Finger et al., 1981). Interconnections of NL (and likely also of PGd) with the valvula maintain topography. The medial valvula was recognized physiologically as related to mormyromast/ampullary organ information (VamMA; Russell & Bell, 1978). Unique among vertebrates is a direct connection of this electrolocation-related medial leaf of the valvula to the pallial telencephalon in mormyrids (lateroposterior pallial zone; Dlp; Wullimann & Rooney, 1990). Alternatively, ampullary organ/mormyromast information may reach the pallium via the medial toral nucleus (MV), since the latter receives ELL cortex input and projects to PGv, which, in turn has extensive projections to the pallium (Fig. 9c, d; Wullimann & Northcutt, 1990; von der Emde & Prechtl, 1999).

Regarding knollenorgan (electrocommunication) pathways (Fig. 9d), the nucleus of the ELL projects (non-topographically) to the anterior exterolateral toral nucleus (NEa), with collaterals to the MV (Enger et al., 1976;

Fig. 10 (continued) fascicle, MO medulla oblongata, MON medial octavolateralis nucleus, MV ventral nucleus of torus semicircularis, MZ medial zone of ELL, NE, NL, exterolateral, lateral nucleus of torus semicircularis, nELL nucleus of the ELL, ON optic nerve, PEd, PEv dorsal, ventral preeminential nucleus, PG preglomerular complex, PGd dorsal preglomerular nucleus, PGv ventral preglomerular nucleus, Pit pituitary, Tel telencephalon, TeO tectum opticum, TH tuberal hypothalamus, TLo torus longitudinalis, TS torus semicircularis, TT toro-preeminential tract, TV toro-valvular tract, V ventricle, Val, Vam lateral, medial leaf of valvula cerebelli, VLZ ventrolateral zone of ELL, VP ventroposterior nucleus of torus semicircularis

Szabo et al., 1983; Bell & Szabo, 1986). In MV, therefore, knollenorgan and mormyromast/ampullary organ information converges and both may reach via PGv the telencephalic pallium (see above; Fig. 9d). Moreover, the NEa synapses on neurons of the posterior exterolateral nucleus (NEp) which projects to an isthmic granular population (IG) ventral to PE and to MV. Interestingly, different from the medial valvular mormyromast/ampullary organ region (VamMA), a lateral valvular area has been shown physiologically to be knollenorgan related (ValK; Russel & Bell, 1978) and the latter receives differential input from the isthmic granular population and from MV (Haudegé-Carré, 1979; Finger et al., 1981; Bell & Szabo, 1986). Whether the ValK also projects directly to the telencephalon is unknown.

Critical for mormyrid descending motor pathways related to the generation of EODs (Carlson, 2002) are corollary discharge pathways which provide information on the reafference (the self-generated electric signal) to the ELL in addition to the primary sensory exafference (signals emitted by conspecifics). These corollary pathways filter out self-generated signals via inhibition in the nucleus of the ELL and also act in the ELL cortex in the discrimination of reafference versus exafference (Heiligenberg, 1984; Bell and Szabo, 1986; Meek & Grant 1994).

As mentioned above, the MON (Fig. 10a; previously anterior lateral line lobe; Bell, 1981a; Haugedé-Carré, 1983) receives primary octaval (medially) as well as lateral line mechanosensory projections (laterally) and its efferent connections thus, include auditory as well as mechanosensory pathways (Fig. 9b). However, these are segregated up into the mediodorsal toral nucleus (MD; Bell, 1981b; Haudegé-Carré, 1983; Kozloski & Crawford, 1998). The MON also has less massive collateral projections to the ventroposterior toral nucleus (VP) and reciprocal connections with the small ventral preeminential nucleus (PEv; Fig. 10b). The ascending connections of MD (both auditory and mechanosensory) and VP reach the ventral preglomerular nucleus (PGv; Bell, 1981b; von der Emde & Prechtl, 1999) which, in turn, projects to the pallium (Wullimann & Northcutt, 1990). Sensory evoked potentials and multiunit spike responses in extensive medial, central and lateral pallial areas (Dm, Dc, Dl) have demonstrated that the mormyrid telencephalic pallium displays largely unimodal sensory fields (visual, auditory, electrosensory and mechanosensory lateral line), with minor overlapping (multimodal) areas (Prechtl et al., 1998). Furthermore, nonoverlapping anterior auditory and posterior mechanosensory portions of the medial pallial area (Dm) both receive input from (presumably different cells within) PGv (von der Emde & Prechtl, 1999), leaving no doubt that mechanosensory lateral line, as well as auditory, information reaches the pallium via PGv. The MD and PGv have also efferents to the medial cerebellar valvula (Finger et al., 1981). With the exception of these valvular connections, the mechanosensory lateral line circuitry just described is highly comparable to such pathways seen in other (electrosensory and non-electrosensory) teleosts (compare Fig. 9 to Figs. 6–8). In summary, the mormyrid brain is highly consistently documented both physiologically and anatomically to display parallel lateral line (and octaval) sensory pathways ascending in parallel from brain stem to telencephalic pallium.

Beyond the remote phyletic distribution of weakly electric organs and multiple electroreceptor types in distantly related mormyrids and gymnotoids, various differences in their nervous systems reveal an independent evolutionary origin. In gymnotoids all electroreceptors (but not the mechanoreceptive neuromasts) are innervated exclusively by the anterior lateral line nerve root (Fig. 8), whereas in mormyrids (and ironically in silurids), the head electroreceptors are innervated by the anterior and those of the body trunk by the posterior lateral line nerve root (Figs. 7, 9). Whereas the electrosensory torus semicircularis (TSl) is laminated in gymnotoids (Fig. 8), it is subdivided into distinct nuclei in mormyrids (NL, NEa, NEp, MV; Fig. 10). An enlargement of the cerebellum occurs in both groups, involving the corpus cerebelli in gymnotoids (Fig. 8) and the valvula cerebelli in mormyrids (Figs. 9, 10).

Unique among electrosensory teleosts is that the cerebellar valvula (and corpus, i.e., C3) in mormyrids receives input from various centers of the ascending pathways of mechanosensation, electrolocation and electrocommunication (Figs. 9b, c, d; Finger et al., 1981; Meek et al., 1986). These interconnections with the cerebellum clearly represent a specialisation of mormyrids (Wullimann & Northcutt, 1990). This teleost family has extraordinarily large brains (Fig. 9a) and the major reason for it is the gigantic cerebellar valvula (Meek et al., 1992, 2008), half of which is involved with electrosensory processing (Finger et al., 1981, Bell & Szabo, 1986; see above).

Furthermore, the connections from midbrain to forebrain differ somewhat between gymnotoids and mormyrids. A diencephalic preglomerular nucleus (PGl, PGv) is always involved at the diencephalic level in the ascending mechanosensory lateral line pathways in teleosts (Figs. 6–9). This also seems to apply for electrosensory pathways in silurids and gymnotoids (PGl), although a (pretectal) nucleus electrosensorius is synaptically intermittent in these groups. In mormyrids, one (minor) electrosensory pathway runs via MV and PGv to pallium. However, the preglomerular nucleus recipient of the bulk of electrolocation information (PGd) does not project to the pallium, but instead seems to reach the telencephalon only via the medial cerebellar valvula (Fig. 8c). Thus, the mormyrid PGd/PGv may have arisen from an ancestral, soley mechanosensory population. These and many other differences corroborate the phylogenetic fact that mormyrids and gymnotoids do not share a common ancestor with the physical outfit necessary for active electrolocation.

5 Lobe -Finned Fishes: Coelacanths, Lungfishes, Amphibians

Lobe finned-fishes (sarcopterygians) include all fossil and extant lungfishes and actinistians (i.e., the coelacanth *Latimeria chalumnae*; Fig. 1), as well as all solely fossil lobe-finned fish taxa, for example the osteolepiforms. Among the latter fossils are those most closely related to tetrapods which themselves are included in the sarcopterygians (Fig. 1). All non-tetrapod sarcopterygians possess both components of the ancestral lateral line system, i.e., electrosensitive ampullary organs as well as mechanosensitive canal and free neuromasts, clearly sharing common ancestry within vertebrates (Bemis & Hetherington, 1982; Jørgensen, 1991; Northcutt & Bemis, 1993). Among sarcopterygians, only lungfishes have ampullary organs on the trunk in addition to the head (Northcutt, 1986b). Among tetrapods, only amphibians display an electrosensory (ampullary organs) and mechanosensory (free neuromasts, but never lateral line canals) lateral line system (Fritzsch, 1989; Schlosser, 2002). Most larval and adult urodeles have both electro- and mechanosensory lateral line sensory modalities, with some notable exceptions in plethodontid salamanders (Fritzsch & Münz, 1986; Fritzsch, 1988a, 1989; Northcutt, 1992). Caecilians (gymnophionans) also have ampullary organs and neuromasts as larvae, but lose them as adults (Hetherington & Wake, 1979; Fritzsch et al., 1985; Fritzsch & Münz, 1986). Larval gymnophionans of the genus *Typhlonectes* only have ampullary organs, but no neuromasts (Fritzsch, 1989). Anurans never have ampullary organs, but anuran tadpoles retain a mechansosensory lateral line system. In various anuran taxa (mostly in pipids) the mechanosensory lateral line system is maintained into adulthood, for example in the African clawed frog *Xenopus laevis*. This retention is correlated with an adult aquatic lifestyle and is likely a secondary reversal within anurans (Fritzsch et al., 1987; Fritzsch, 1988b). Thus, an electrosensory and mechanosensory lateral line system is basally present in amphibians. In contrast, all amniotes lack any trace of lateral line peripheral and central nervous structures and these are believed to have been lost with the terrestrial life style (notably independently of similar losses in amphibians).

In all extant sarcopterygians, lateral line electroreceptors and mechanoreceptors coincide with the presence of a DON and a MON, respectively in the octavolateralis area dorsal to the octaval column (Northcutt, 1980b, 1986b; Fritzsch, 1988a, b; Will, 1989). However, almost nothing is known regarding the central anatomy of the lateral line system in non-tetrapod sarcopterygian and the focus will therefore be on (tetrapod) amphibians. As in the basal gnathostome pattern, larval and adult urodeles and larval gymnophionans have electrosensory ganglion cells only in the anterior lateral line nerve and these fibers enter the DON via the dorsal root (Fig. 11; Fritzsch, 1981; Fritzsch et al., 1985; Fritzsch, 1988a, b). Naturally, anurans lack this electrosensory projection, but anuran tadpoles and some adult forms (see above) share with gymnophionans and urodeles primary mechanosensory lateral line projections which reach via ALLN and PLLN the MON (usually called intermediate nucleus in amphibians), and the small eminentia granularis (Fig. 11; Fritzsch et al., 1984; Will et al., 1985a; Simpson et al., 1986). Octaval (saccular) projections reach also the most ventral zone of the intermediate nucleus. Overall, urodeles represent best the ancestral situation of the lateral line system in amphibians.

In adult *Xenopus laevis*, second order connections of the lateral line related intermediate nucleus, apart from commissural projections, consist of the main ascending lateral lemniscal projection to the ventrally located magnocellular

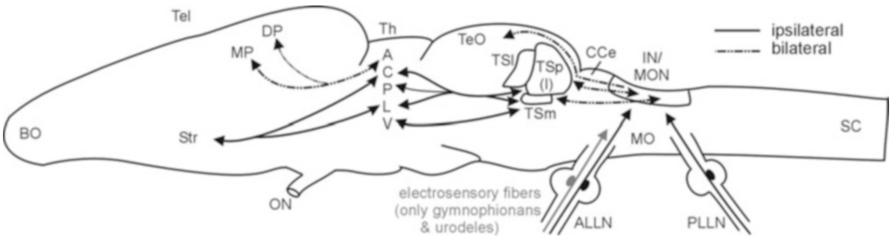

Fig. 11 Schematic lateral view of the brain of *Xenopus laevis* (after Edwards and Kelley, 2001) with mechanosensory lateral line pathways indicated (see text for citations). Grey arrow indicates primary electrosensory input in gymnophionans and urodeles from head ampullary organs to dorsal octavolateralis nucleus (not shown); its higher order connections are unknown. Note that MON (IN) has commissural connections (Will, 1988, 1989), that all parts of the torus semicircularis project to the optic tectum (Zittlau et al., 1988), and that the optic tectum projects to the lateral thalamus, all of which is not indicated in the figure. Primary projections after Lowe and Russell (1982) and Altman & Dawes (1983). Abbreviations: A, C, L, P anterior, central, lateral, posterior dorsal thalamic nucleus, ALLN anterior lateral line nerve, BO bulbus olfactorius, DP dorsal pallium, IN intermediate nucleus (=MON), MO medulla oblongata, MON medial octavolateralis nucleus, MP medial pallium, ON optic nerve, PLLN posterior lateral line nerve, SC spinal cord, Str striatum, Tel telencephalon, TeO tectum opticum, Th thalamus, TSl, TSm, TSp laminar, principal, magnocellular nucleus of torus semicircularis, V ventral thalamus

nucleus of the torus semicircularis (TSm) and, less extensively, to the optic tectum (Fig. 11; Will et al., 1985b; Zittlau et al., 1988; Will 1989). However, both neuroanatomy as well as neurophysiology in *Xenopus* indicates that, in addition to TSm, also the lateral part of the principal toral nucleus (TSp(l)) receives lateral line input from the intermediate nucleus (Lowe, 1986; Edwards & Kelley, 2001; Behrend et al., 2006). Both TSm and TSp have reciprocal connections with diencephalic nuclei, including strong ones with the central and lateral dorsal thalamic nuclei, and weak ones with the posterior dorsal thalamic nucleus, as well as with the ventral thalamus (Fig. 11; Edwards & Kelley, 2001). There are also efferent octavolateralis central cells innervating neuromasts in the amphibian lateral line system (Will, 1982; Münz & Claas, 1991).

In adult anuran species lacking a lateral line system, these midbrain toral and diencephalic thalamic divisions remain and serve auditory functions, with a central toral nucleus being the main recipient of ascending auditory brain stem projections (Feng & Lin, 1991; Luksch & Walkowiak, 1998) and a lateral toral nucleus (TSl) being the main auditory output to the central thalamic nucleus, but also to lateral, posterior and anterior thalamic nuclei and to the ventral thalamus (Hall & Feng, 1987; Wilczynski, 1988; Neary, 1988;). This indicates that none of the anuran toral nuclei are exclusively associated with lateral line processing. Finally, central and lateral dorsal thalamic nuclei project heavily to the anuran striatum (Wilczynski & Northcutt, 1983a), while the anterior dorsal thalamic nucleus projects to the medial and dorsal pallium (Neary, 1984; Laberge & Roth, 2007; Laberge et al., 2008), the latter most likely providing information of multisensory nature. These telencephalo-thalamic connections are reciprocal (Wilczynski & Northcutt, 1983b; Westhoff & Roth, 2002). Thus, the telencephalic striatum may be reached through ascending connections of central and lateral thalamic nuclei also in *Xenopus* and convey lateral line information (Fig. 11). However, it remains unresolved if and where lateral line information is separately processed in the dorsal thalamus and striatum and, furthermore, how it would eventually reach pallial levels in anurans. In axolotls, mechano- and electrosensory stimuli lead to evoked potential or multiple unit responses only in the striatum, not in the medial pallium (Northcutt & Plassmann, 1989) which is consistent with the thalamo-telencephalic connections in anurans discussed above (see Fig. 11). The optic tectum in axolotls contains visual, as well as electrosensory and mechanosensory topographical maps (Bartels et al., 1990). Thus, it is also possible that lateral line information in amphibians reaches the striatum via a tecto-thalamic pathway. Overall, the situation in amphibians strongly contrasts with that in amniotes, where ascending sensory projections run via the thalamus to the dorsal pallium.

6 Conclusions and Summary

Despite variability in the craniate range of the mechanosensory and electrosensory lateral line periphery (see Chapter by Webb), there is a basal pattern of primary projections to the octavolataralis area. Generally, octaval (VIIIth nerve), mechanosensory and electrosensory fibers (lateral line nerves) terminate in a non-overlapping manner in their primary central nervous octavolateralis projection zones, i.e., ventral, intermediate and dorsal columns, respectively. Nevertheless, there are various cases of limited to more extensive overlap of mechanosensory and octaval projections both in the intermediate column and ventral column, as noted above for various taxa. The functional significance of these cases is discussed in a companion chapter (Braun & Sand).

The ancestral gnathostome pattern of how lateral line nerves enter the primary nuclei is that a dorsal root of the anterior lateral line nerve complex contains the electrosensory fibers (whose cell bodies are in anterior lateral line nerve ganglia), which terminate in the DON. This pattern is seen in cartilaginous fishes (Fig. 3), in non teleost ray-finned fishes (polypteriforms and chondrosteans) and, notably, in amphibians (urodeles and gymnophionans; Fig. 11). Teleost electroreception evolved newly after its loss in the ancestor of lepisosteiforms (gars) and amiiforms (bowfins; Fig. 5) and, not surprisingly, there is manifold deviation from the ancestral pattern just described. Teleostean electrosensory fibers may be in both anterior and posterior lateral line nerve ganglia (silurids, Fig. 7; mormyrids, Fig. 9), or only in the anterior lateral line nerve ganglion (gymnotoids, Fig. 8). The teleostean primary electrosensory lateral line lobe (ELL) is positionally and histologically different not only from the DON, but also between electrosensory teleosts, reflecting on convergent multiple evolutionary origins, which is also evident in differences of ascending pathways as discussed above. Lampreys too have electrosensory fibers only in the anterior lateral line nerve ganglion complex (Fig. 2), strongly resembling the ancestral gnathostome pattern; their electrosensitive end buds, however, may or may not be homologous to ampullary organs.

Mechanosensory lateral line fibers always are contained both in anterior and posterior lateral line nerve ganglia in all craniates and project primarily to MON (Figs. 3–11). Myxinoids (eptatedrids), like most teleosts, have only a mechanosensory lateral line system, but no electrosensory system, indicating that the electrosense only evolved with the vertebrates, not the craniates (Fig. 1).

Regarding the functional neuroanatomy of ascending (lateral lemniscal) lateral line connections in craniates, the following may be said. Starting with the lateral line primary sensory nuclei (DON, MON), there is a parallel pattern of connectivity up to the midbrain in cartilaginous and ray-finned fishes. Predominant contralateral MON (and when present) DON projections reach the posterior alar midbrain (torus semicircularis). Ray-finned fishes have a feedback circuit via the preeminential nucleus, and nucleus B of cartilaginous fishes may be its homologue. While MON/DON projections to the torus semicircularis are also present in lampreys and amphibians, a feedback loop through a preeminential nucleus has not been desribed in either group. Since there is an uninterrupted anamniote evolutionary history of the mechanosensory lateral line system, its area of representation in the torus semicircularis may be concluded to be homologous among all (anamniote) craniates. The same may be said about the toral electrosensory centers with the exception of those in teleosts that arose newly.

More difficult is the situation in the diencephalon. Here three general areas are involved in lateral line processing: dorsal thalamus, posterior tuberculum and hypothalamus. In cartilaginous fishes – depending on the group – only one midbrain toral recipient nucleus, the posterior lateral thalamic nucleus (PLT; posterior tuberculum) has been described as (sharks and skates), while in rays, additionally to a PLT (electrosense), a posterior central thalamic nucleus (PCT; dorsal thalamus, mechanosense) has been noted (Fig. 4). The batoid hypothalamic lateral tuberal nucleus (mechanosense) does not have projections to the telencephalon. Thus, a key question remains whether and how parallel processing of lateral line electrosense and mechanosense does occur in the diencephalon of cartilaginous fishes.

Interestingly, in non-electrosensory teleosts and basal ray-finned fishes (as far as known), three diencephalic areas are also recipient of midbrain toral input, (1) the dorsal part of lateral preglomerular nucleus (PGld, posterior tuberculum), (2) the central posterior thalamic nucleus (dorsal thalamus) and (3) the anterior tuberal nucleus (hypothalamus). However, the major origin of lateral line projections to forebrain pallial areas (Dm: pallial amygdala; Dl: hippocampus homologue) is from the PGld. An unresolved question is whether the teleostean preglomerular area is of alar plate dorsal thalamic origin (Ishikawa et al., 2007) or of multiprosomeric alar and basal plate origin (Mueller & Wullimann, 2002), a question that will only be decided by fate studies. In silurids, gymnotoids and mormyrids, the lateral preglomerular area acquires a role as the main diencephalic projection area to the pallium which evolved independently for the electrosensory system in each taxon.

Lampreys and amphibians were reported to have a lateral line relay to the telencephalon in the dorsal thalamus only.

Finally, the major projection zones for electrosensory and mechanosensory lateral line information in the telencephalon would seem to be in the medial pallium (hippocampus homologue), at least in lampreys, cartilaginous fishes and ray-finned fishes (Dl). In teleosts, the pallial amygdala homologue (Dm) is an additional major projection zone. In contrast, lateral line information in amphibians relayed in the dorsal thalamus appears to reach the (subpallial) striatum only (although multimodal visual/auditory projections and maybe indirect lateral line projections via optic tectum do reach the medial pallium via the anterior thalamic nucleus).

Presently, our current state of knowledge on functional neuroanatomy of the craniate lateral line system does not allow for clearly establishing its ancestral pattern of ascending diencephalo-telencephalic connections. The medial pallium (hippocampus homologue) in all gnathostomes likely receives lateral line diencephalic input (mainly from posterior tuberculum and/or dorsal thalamus) ancestrally. However, tetrapods (amphibians) appear then to have lost diencephalo-pallial lateral line projections, but developed input to the subpallial striatum. Alternatively, lampreys, cartilaginous fishes, ray-finned fishes and lobe-finned fishes acquired mechano and electrosensory lateral line input to the telencephalon independently in evolution.

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