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Photographs of adult honey possums in their native habitat. Dunlop, Ross and Beazley (p. 309).

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Descending Telencephalic Information Reaches Longitudinal Torus and Cerebellum via the Dorsal Preglomerular Nucleus in the Teleost Fish, *Pantodon buchholzi*: A Case of Neural Preaptation?

Key Words

Cerebellum
Diencephalon
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Evolution
Fish
Mechanoreception
Motor systems
Telencephalon
Teleost
Torus longitudinalis

Abstract

The weakly electric mormyrids are known to have an ascending neuronal pathway that reaches the diencephalon and carries information concerned with electrolocation. The recipient diencephalic center, the dorsal preglomerular nucleus, receives a massive telencephalic input and projects to the corpus and valvula cerebelli. This circuitry has been interpreted as a uniquely derived (autapomorphic) feature for mormyrids. In the present study, we demonstrate with the fluorescent neuronal tracer DiI that the closely related, but non-electroreceptive, teleost *Pantodon buchholzi* possesses a dorsal preglomerular nucleus with similar telencephalo-cerebellar circuitry. The projection to the cerebellum only reaches the corpus, however, not the valvula cerebelli. Further, the dorsal preglomerular nucleus of *Pantodon* displays a descending pathway via the torus longitudinalis. Two phylogenetic interpretations for the presence of telencephalo-cerebellar pathways in both mormyrids and *Pantodon* are possible: if such a pathway existed as a preaptation in the common ancestor of mormyrids and *Pantodon*, it must be an exaptation for electroreception in mormyrids, since this sensory modality evolved anew in this teleost group; alternatively, the pathway evolved in parallel homoplasy, once in *Pantodon*, as part of a descending premotor pathway, and independently in mormyrids, where the system gains access to ascending electrosensory information.

Introduction

Teleost fishes represent more than half of the extant vertebrate species. They can be grouped into four major clades [after Lauder and Liem, 1983; fig. 1a]: the Osteoglossomorpha (see below), the Elopomorpha (ladyfishes), the Clupeo-

morpha (herrings and anchovies), and finally, the Euteleostei (including the most speciose teleost groups such as the ostariophysines and percomorphs).

Osteoglossomorphs comprise two subdivisions (fig. 1b), the Osteoglossoidae and the Notopteroidei. The osteoglossoids include the South American *Osteoglossum* and *Ara-*

List of Abbreviations Used

Ce	corpus cerebelli	NT	nucleus taenia
CP	central posterior thalamic nucleus	Oc	oculomotor neurons
CPN	central pretectal nucleus	OT	optic tract
Dc	central zone of area dorsalis telencephali	p	Purkinje-cell layer of cerebellum
Dd	dorsal zone of area dorsalis telencephali	PCo	posterior commissure
DI	lateral zone of area dorsalis telencephali	PE	preeminential nucleus
Dla	lateral part of DI	PGd	dorsal preglomerular nucleus
Dlb	intermediate part of DI	PGm	medial preglomerular nucleus
Dlc	ventral part of DI	PGr	rostral preglomerular nucleus
Dlp	posterior part of DI	PGv	ventral preglomerular nucleus
Dm	medial zone of area dorsalis telencephali	pgz	periventricular gray zone of optic tectum
do	dorsal layer of torus longitudinalis	PL	perilemniscal nucleus
DT	dorsal tegmental nucleus	PM	nucleus preopticus magnocellularis
ELL	electrosensory lateral line lobe	PO	posterior pretectal nucleus
FR	fasciculus retroflexus	PPd	dorsal part of periventricular pretectal nucleus
g	granular layer of cerebellum	PTT	preglomerulo-toral tract
GS	secondary gustatory nucleus	RL	nucleus rostromedialis of Butler and Saidel [1991]
Hy	periventricular anterior tuberal hypothalamus	TA	anterior tuberal nucleus
in	intermediate layer of torus longitudinalis	TeO	tectum opticum
l	lateral forebrain bundle	TH	tuberal hypothalamus
LC	nucleus of the locus coeruleus	TL	torus longitudinalis
LI	inferior lobe of hypothalamus	TPT	telencephalo-preglomerular tract
LL	lateral longitudinal fascicle	TPp	periventricular nucleus of posterior tuberculum
LLN	lateral line nerves	TS	torus semicircularis
LM	medial longitudinal fascicle	v	ventrolateral optic tract
m	molecular layer of cerebellum	Va	valvula cerebelli
ma	marginal layer of optic tectum	Vam	medial leaf of valvula cerebelli
MON	medial octavolateralis nucleus	Vd	dorsal zone of area ventralis telencephali
NId	dorsal portion of nucleus interpeduncularis	ve	ventral layer of torus longitudinalis
Nlv	ventral portion of nucleus interpeduncularis	Vv	ventral zone of area ventralis telencephali
NL	lateral nucleus of torus semicircularis	VMr	rostral part of ventromedial thalamic nucleus
NLV	nucleus lateralis valvulae		

paima, as well as the Asian *Scleropages*, and the African *Pantodon* and *Heterotis*. The second osteoglossomorph subdivision, the notoapteroids, also have representatives in the New World (*Hiodon*) and in the Old World (mormyrids, notoapterids).

Mormyrids are weakly electric fish that have the ability not only to detect external electric fields but to electrolocate objects and to electrocommunicate with conspecifics by way of self-generated electric signals. It is generally accepted that in mormyrids (and in a few additional teleost groups) the electrosense is newly evolved, since the phylogenetically primitive (plesiomorphic) electrosensory modality was lost early in the evolution of ray-finned fishes [Bullock et al., 1983].

The dorsal preglomerular nucleus of the mormyrid *Gnathonemus petersi* is likely involved in electrolocation (see fig. 8c and Discussion). Ascending information from mor-

myromasts (the electroreceptors that are known to detect this kind of electrosensory information) reaches the electrosensory lateral line lobe [Bell and Russell, 1978; Bell, 1981] and is relayed via the lateral nucleus of the torus semicircularis to the dorsal preglomerular nucleus [Bell et al., 1981; Finger et al., 1981]. This diencephalic nucleus receives additional afferents from the telencephalon [Wullimann and Northcutt, 1990] and projects to both the corpus [Meek et al., 1986] and the valvula cerebelli [Finger et al., 1981]. Within the valvula, the projection from the dorsal preglomerular nucleus is restricted to the medial leaf, which is involved in the processing of electrolocation [mormyromast-ampullary region of Finger et al., 1981]. Finally, the medial leaf of the valvula projects to the telencephalon [Haugedé-Carré, 1980; Wullimann and Rooney, 1990]. Since electroreception developed anew in mormyrids, the described circuitry has been interpreted as being derived

(apomorphic) for *Gnathonemus* [Wullimann and Northcutt, 1990]. A similar circuitry is therefore not to be expected in non-electroreceptive osteoglossomorphs.

Recently, it was demonstrated with horseradish peroxidase (HRP) tracing that the non-electrosensory osteoglossomorph *Pantodon buchholzi* possesses a similar dorsal preglomerular nucleus with afferents from the telencephalon and efferents to the corpus cerebelli [Wullimann and Meyer, 1993]. In that study, the nucleus was described and documented cytoarchitectonically and topologically. Because of its location within the preglomerular area, and because of the presence of a telencephalic input and the absence of retinal input [Butler and Saidel, 1991], it was concluded that said nucleus is neither a pretectal nor a dorsal accessory optic nucleus, but is part of the preglomerular area. Three different telencephalo-cerebellar relay nuclei have been described in the diencephalon of various teleosts [Ito et al., 1982; Wullimann and Northcutt, 1990], and the dorsal preglomerular nucleus of *Pantodon* and *Gnathonemus* represents one of them, which – in contrast to the other two – evolved only in osteoglossomorphs [Wullimann and Meyer, 1993].

In the present study, we investigated the connections of the dorsal preglomerular nucleus of *Pantodon* with the carbocyanine dye DiI in order to confirm the telencephalic and cerebellar connections and to reveal additional connections of the nucleus.

A preliminary report on the data herein was presented at the 11th J.B. Johnston Club Meeting in New Orleans, November 1991, and an abstract was published subsequently [Wullimann and Roth, 1992]. The neuroanatomical nomenclature for the diencephalon is that of Braford and Northcutt [1983], as modified by Wullimann and Northcutt [1990] and Wullimann and Meyer [1990]; for the telencephalon, the nomenclature is that of Weston [1937] as modified by Nieuwenhuys [1963].

Materials and Methods

A description of the tracing experiments with DiI will be followed by a section on the preparation of the normal anatomical material. All animal research described in this study was approved by the Senat of the city of Bremen, Germany.

DiI Experiments

Specimens of *Pantodon buchholzi* were deeply anesthetized with tricaine methanesulfonate salt (MS 222; Sigma, Deisenhofen, Germany) before they were transcardially perfused with cold 0.1 M phosphate buffer (PB; pH = 7.4) followed by cold 4% paraformaldehyde in PB. The brains were taken out of the crania and postfixed in 4% paraformaldehyde at 4 °C for 2 to 15 days. Thereafter, small crystals of the carbocyanine dye DiI (1,1'-dioctadecyl-3,3,3',3'-tetramethylindo-

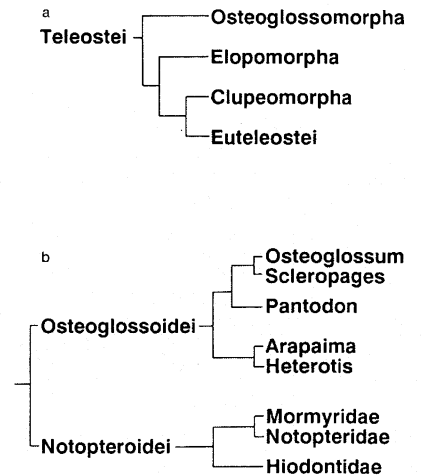


Fig. 1. Cladograms showing phylogenetic relationships of extant major teleost clades (a) and osteoglossomorph teleosts (b) according to Lauder and Liem (1983).

carbocyanine perchlorate; Molecular Probes, Eugene, OR) were placed into the telencephalon, the corpus cerebelli, the dorsal preglomerular nucleus, or the torus longitudinalis. In the case of the torus, part of the ipsilateral optic tectum had to be ablated prior to DiI deposition. In order to prevent subsequent displacement of the DiI crystals, the application site was sealed with 4% agar-agar (Merck, Darmstadt, Germany). The brains were then incubated, either at room temperature from 27 to 285 days or at 40 °C from 7 to 100 days, before they were embedded in 4% agar-agar and cut on a vibratome at a thickness of 50 µm. The sections were collected in 0.1 M PB and mounted with 95% glycerol in PB. The DiI-material was then analyzed with a rhodamine type filter and phase contrast optics. The original method for DiI tracing in fixed tissue was published by Godement et al. [1987].

Normal Anatomy

A series of transverse brain sections of *Pantodon buchholzi*, stained according to the Bodian silver method [Romeis, 1989] and counterstained with cresyl violet, was prepared for comparison with the DiI-material.

In addition, the brains of a few fixed specimens of *Arapaima gigas* – generously donated by Dr. F. Krupp and the Forschungsinstitut Senckenberg, Frankfurt a.M., Germany – were taken out of the crania, transferred to 70% ethanol for 24 h and then cryoprotected for 5 days in PB containing 30% sucrose. Thereafter, the brains were cut on a cryostat at 25 µm and stained with cresyl violet.

Results

The DiI was deposited in one of several divisions of the telencephalon of *Pantodon* (for externally visible divisions see fig. 8a): in the corpus cerebelli, in the dorsal preglomer-

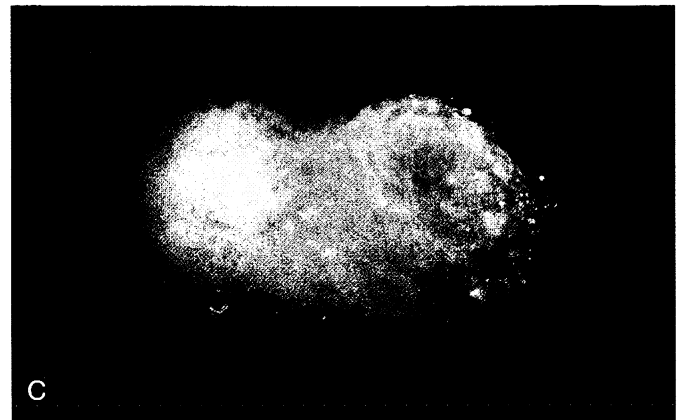
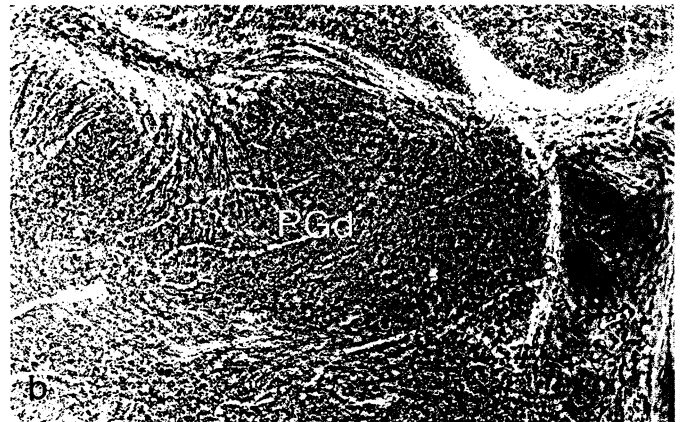
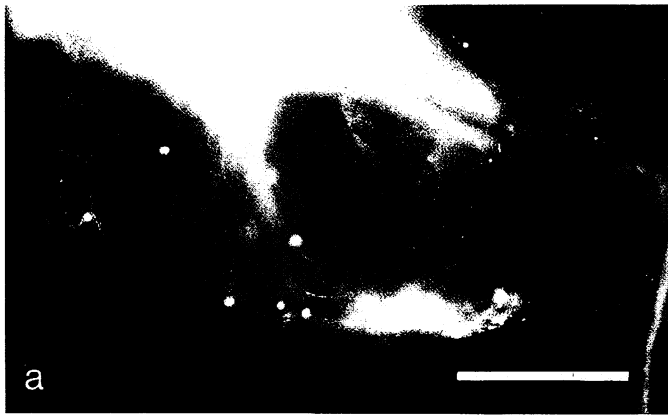


Fig. 2. Photomicrographs of transverse sections through the dorsal preglomerular nucleus of *Pantodon* showing: **a** retrogradely labeled neurons after DiI deposition into the corpus cerebelli, **b** the same section in phase contrast, and **c** terminal field after DiI deposition into the telencephalon. Lateral is to the right in this and all other figures. For orientation note that level of section is similar to that shown in figure 3d. Bar in **a** = 0.1 mm for **a–c**.

ular nucleus or in the torus longitudinalis. It is beyond the scope of the present paper to report the differential connections of the various subdivisions of the telencephalon with the rest of the brain. Only those findings related to the circuitry of the dorsal preglomerular nucleus will be mentioned. All connections are ipsilateral, unless otherwise noted.

Application of DiI to the corpus cerebelli results in retrogradely labeled neurons in the dorsal preglomerular nucleus, most of which are located at the periphery of the nucleus (fig. 2a, b). Application of DiI to the telencephalon, including the central zone of area dorsalis telencephali (Dc), always results in a heavy terminal field within the dorsal preglomerular nucleus throughout its rostrocaudal extent (fig. 2c).

Deposition of DiI in the dorsal preglomerular nucleus confirms these two connections (fig. 3a, e). Many neurons are retrogradely labeled in the rostradorsal part of Dc (fig. 3a, 4d), which is closely associated with the dorsal zone of area dorsalis telencephali but also with the more rostral portions of the medial and lateral zones of area dor-

salis telencephali. A restricted dense terminal field occurs in the most rostral portion of the granular layer of the corpus cerebelli (fig. 3e, 4a–c).

Further, the heavily labeled preglomerulo-toral tract exits the dorsal preglomerular nucleus dorsomedially (fig. 3d, 5b, d) and courses towards the torus longitudinalis, where it arborizes into a massive terminal field bilaterally within the intermediate layer (fig. 3c, d, 5a, c). Additional terminals are located in the inferior lobe of the hypothalamus, the rostral and ventral preglomerular nuclei, the rostralateral nucleus of Butler and Saidel [1991], and within the telencephalon in the intermediate part of the lateral zone of area dorsalis telencephali (Dlb).

Following these DiI applications into the dorsal preglomerular nucleus, additional retrogradely labeled cells are located in the magnocellular preoptic nucleus (also contralaterally), in the posterior pretectal and ventral preglomerular nuclei (very sparsely in the latter), and in the medial torus semicircularis, the optic tectum and two brainstem nuclei, locus coeruleus and a second nucleus immediately dorsal to it, which is also retrogradely labeled contralater-

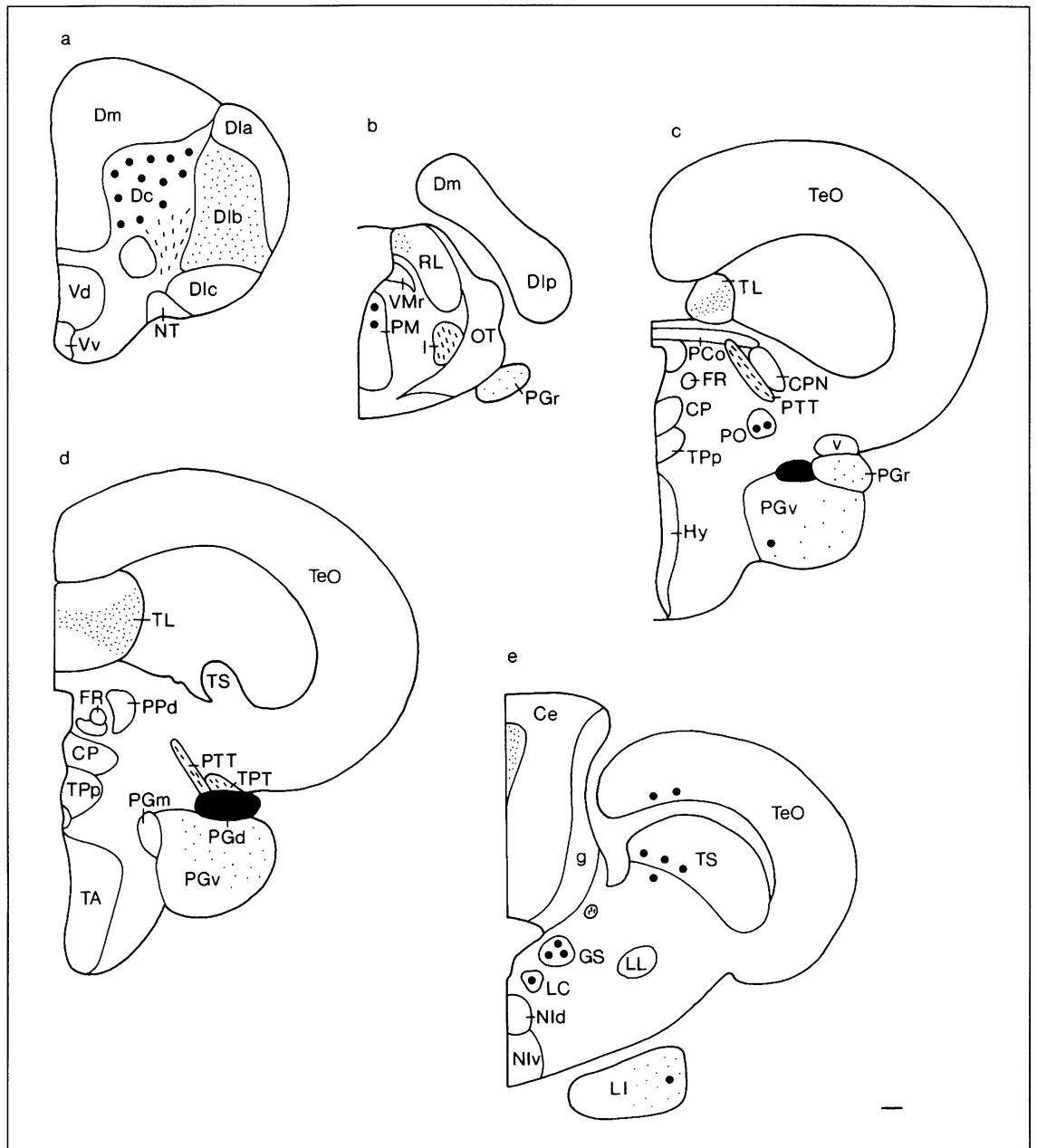


Fig. 3. Chartings of the right sides of transverse sections through the brain of *Pantodon* from telencephalic (**a**) to brainstem (**e**) levels after DiI deposition (black areas in **c**, **d**) into the dorsal preglomerular nucleus. Stippling, labeled terminals; dashes, labeled fiber tracts; large black dots, retrogradely labeled neurons. For abbreviations see list. Bar = 0.1 mm.

ally (fig. 3e). We tentatively identify the latter nucleus as the secondary gustatory nucleus. The contralateral dorsal preglomerular nucleus also contains some labeled terminals and neurons. Further, neurons in the periventricular nucleus of the lateral recess of the inferior lobe were labeled (not depicted).

After DiI application to the torus longitudinalis unilaterally, strong labeling occurred bilaterally in the preglomerulo-torus tract and in most neurons of the dorsal preglomerular nucleus, including those located at the periphery as well as the center (fig. 6a, 7a, b). Many labeled axons diverge from the preglomerulo-torus tract and course caudally

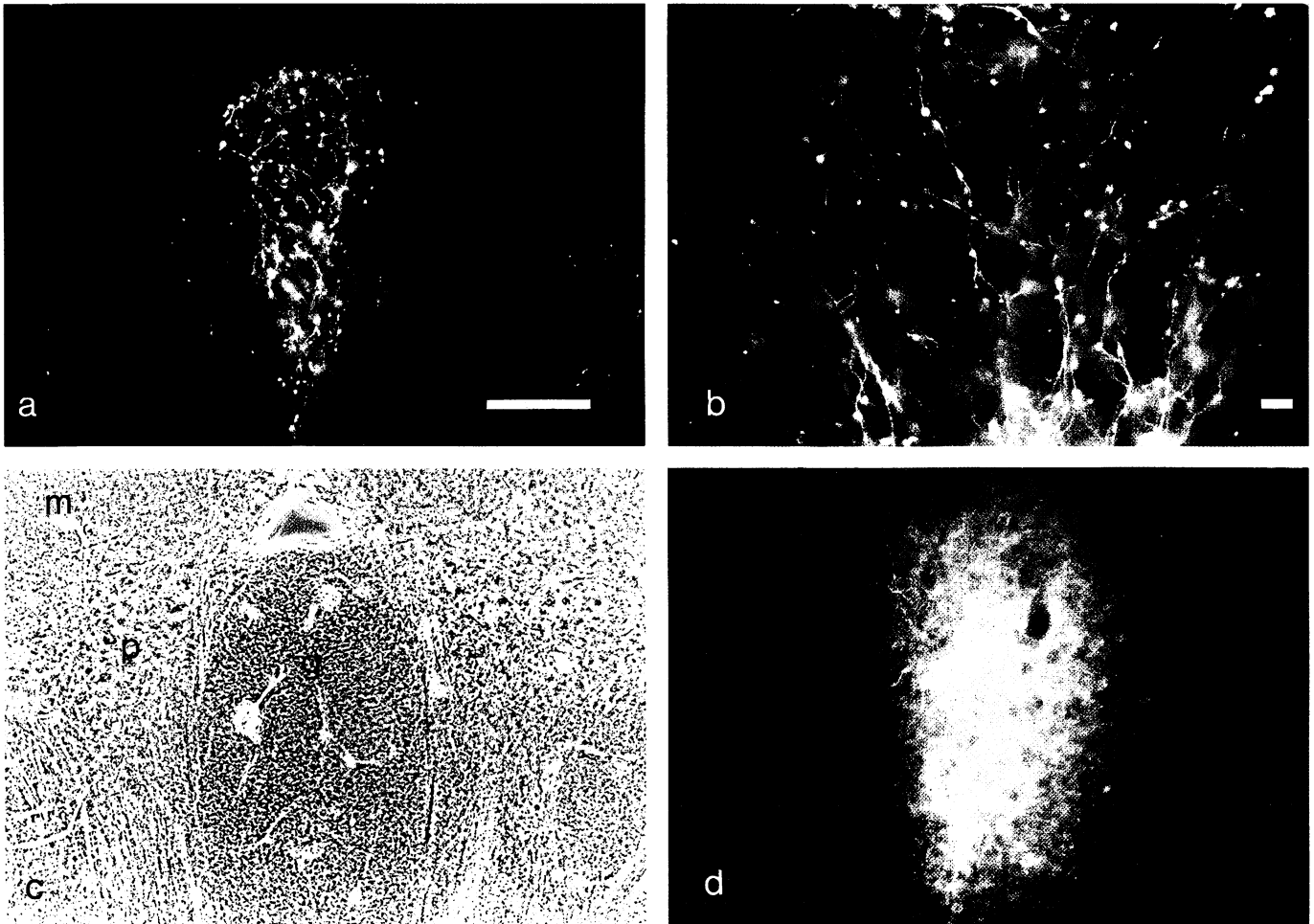


Fig. 4. Photomicrographs of transverse sections through the brain of *Pantodon* showing: **a, b** the terminal field in the granular layer of the corpus cerebelli after DiI deposition into the dorsal preglomerular nucleus; **b** shows fine varicosities of these terminal arborizations at larger magnification; **c** shows the same section as **a** in phase contrast and demonstrates that terminal field is confined to the granular layer; **d** shows the density of retrogradely labeled neurons in Dc after DiI deposition into the dorsal preglomerular nucleus. Level of sections in **a** to **c** is that shown in fig. 2e. Level of section in **d** is rostral to that shown in fig. 2a. Bar in **a** = 0.1 mm for **a, c, d**; bar in **b** = 0.01 mm.

(bilaterally) forming a tegmento-toral tract. The labeled neuronal somata belonging to these fibers are located bilaterally in the dorsal tegmental nucleus, in the nucleus lateralis valvulae, and, further caudally, in the oculomotor area (fig. 6b, 7c, d). Anterogradely labeled fibers also run within the tegmento-toral tract and terminate bilaterally in the granular layer of the rostral corpus cerebelli and, strongly, in the dorsal part of the nucleus interpeduncularis (fig. 6b, 7c, d). Some labeled fibers were present bilaterally in the granular layer of the valvula cerebelli, most likely representing collaterals of the dorsal tegmental nucleus or the nucleus lateralis valvulae. However, no cell somata

were labeled in the valvula. Solely contralaterally, labeled fibers descend via the tecto-bulbar tract and appear to terminate in the mesencephalic reticular formation. Further, neurons and terminals were labeled contralaterally in the torus semicircularis and in a perilemniscal nucleus (in the latter, only neurons were labeled) lying lateral to the lateral longitudinal fascicle. A tract originating in these two nuclei runs from the ventrolateral edge of the contralateral tectum throughout its periventricular gray zone medially and via the intertectal commissure towards the DiI application site (fig. 6). Most likely, the fibers of this tract terminate in the ablated ipsilateral tectum (see Discussion). Additionally,

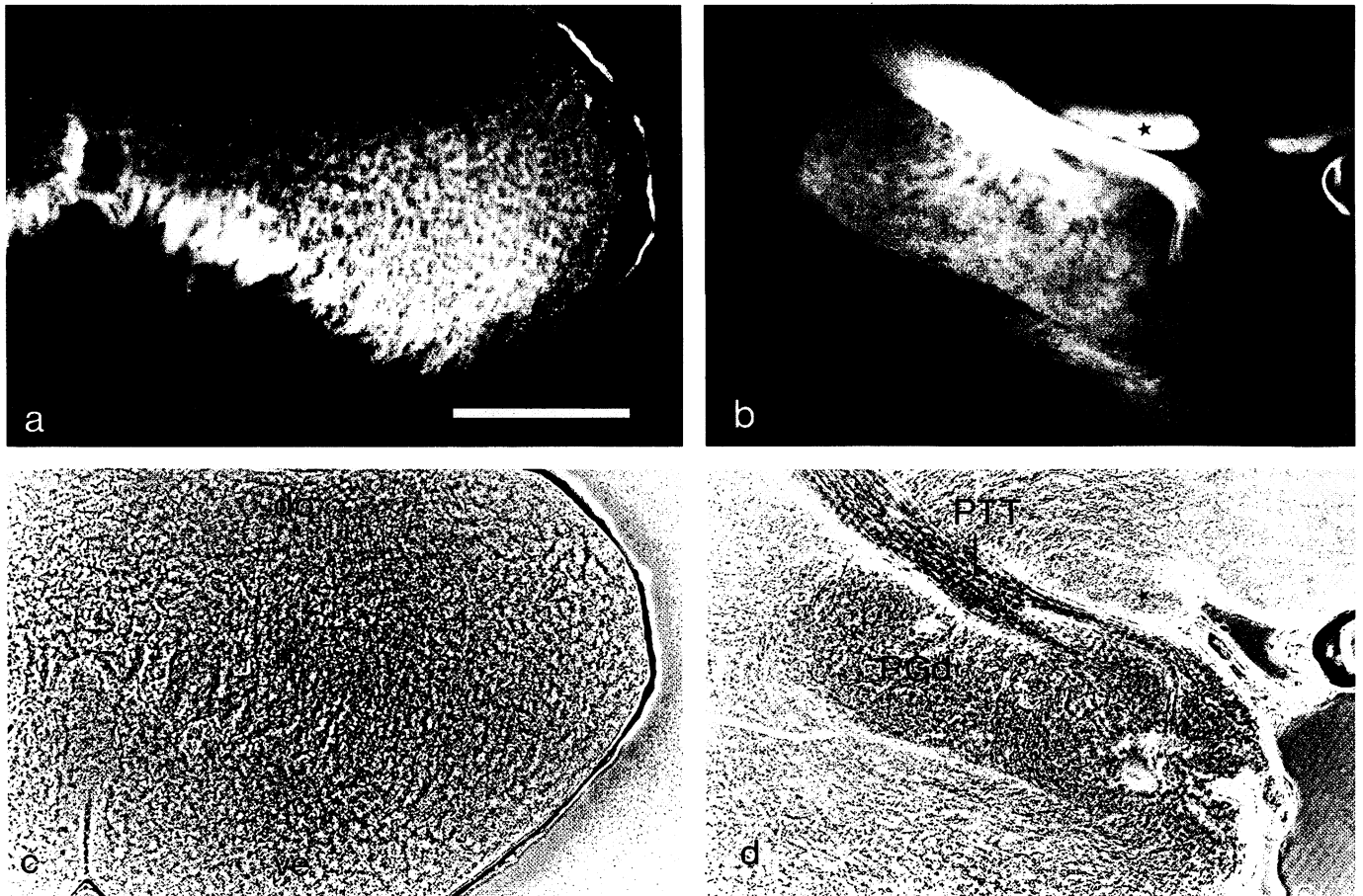


Fig. 5. Photomicrographs of transverse sections through the brain of *Pantodon* showing: **a** terminals in the intermediate layer of the torus longitudinalis after **(b)** DiI application to the dorsal preglomerular nucleus; **c** and **d** show the same respective sections in phase contrast. Level of all sections corresponds to that shown in fig. 3d. Asterisk in **b** and **d** indicates the telencephalo-preglomerular tract which contains the axons of neurons in Dc (see also fig. 4d). Bar in **a** = 0.1 mm for **a–d**.

labeled fibers and terminals were clearly present in the deep white zone overlying the periventricular gray zone and in a layer immediately adjacent to it within the central zone of the contralateral tectum. More peripherally, in the contralateral central and superficial tectal zones, only a few labeled fibers were seen. The ipsilateral tectal tissue immediately lateral to the torus longitudinalis was spared by the ablation, and here, in addition to label similar to that described for the contralateral tectum, strongly labeled terminals were present in the marginal layer (fig. 6a). In the contralateral torus longitudinalis, strongly labeled fascicles traverse the dorsal layer from more dorsally; they form only a dense fiber plexus in the intermediate layer, whereas neurons are also labeled in the ventral layer. A few labeled, thick axons can be followed rostrally into the lateral forebrain bundle and into their neurons of origin in Dc bilaterally.

Discussion

We will first discuss some methodological aspects, before continuing with functional and, finally, evolutionary considerations.

Methodological Aspects

As revealed by DiI application to the dorsal preglomerular nucleus of *Pantodon*, some of the connections of this nucleus (fig. 3) may represent labeling of fibers of passage or of collaterals of retrogradely labeled cell groups. The latter is almost certainly the case for the terminal field in the intermediate part of the lateral zone of area dorsalis telencephali, which likely does not originate in the dorsal preglomerular nucleus. After DiI deposition to the lateral zone of area dorsalis telencephali, including its lateral (Dla) and

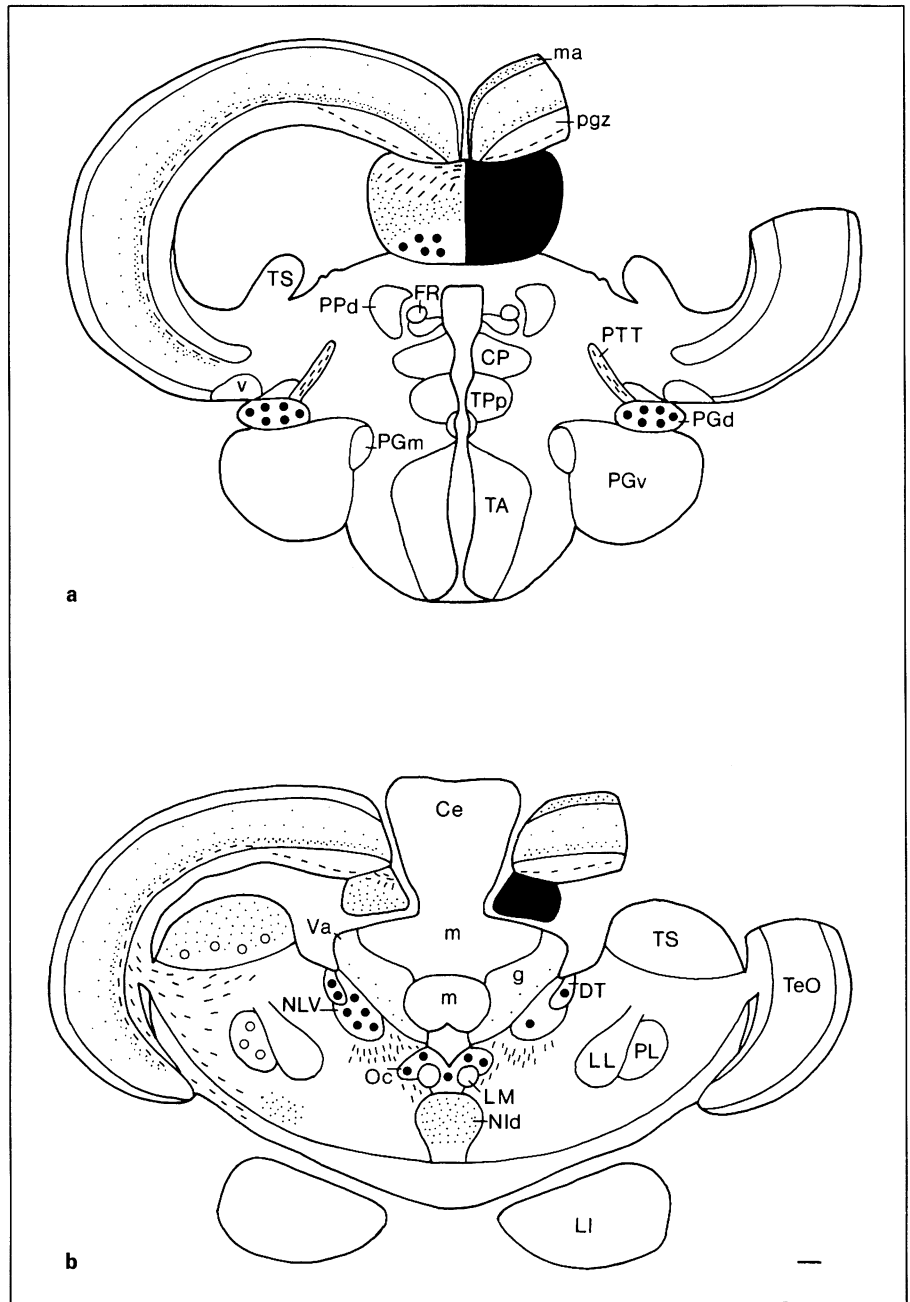


Fig. 6. Chartings of transverse sections through the brain of *Pantodon* after DiI deposition into the torus longitudinalis. Stippling, labeled terminals; dashes, labeled fiber tracts; large black dots, retrogradely labeled neurons; open circles, neurons labeled by interruption of fibers of passage (see text). For abbreviations see list. Bar = 0.1 mm.

intermediate (Dlb) parts in *Pantodon*, neurons in the central zone of area dorsalis telencephali (Dc), but not in the dorsal preglomerular nucleus, are retrogradely labeled, indicating that Dc projects to both Dlb and the dorsal preglomerular nucleus. In further support of this interpretation is the fact that Dc also projects to the lateral zone of area dorsalis telencephali in the percomorph *Sebastiscus marmoratus* [Murakami et al., 1983]. Since the area dorsalis telence-

phali also receives projections from the locus coeruleus in *Pantodon* [M.F. Wullimann, unpubl. observ.], the labeled neurons in the latter nucleus may also be the result of labeling fibers interrupted by DiI application to the dorsal preglomerular nucleus.

A projection from the optic tectum to the nucleus rostro-lateralis was recently described in *Pantodon* [Butler and Saidel, 1992]. The labeled tectal cells and labeled fibers in

nucleus rostrrolateralis may therefore result from labeling of fibers of passage. The same likely applies to labeled cells in the posterior pretectal nucleus and labeled fibers in the inferior lobe, since the posterior pretectal nucleus is known to project heavily to the inferior lobe in the osteoglossomorph *Osteoglossum bicirrhosum* [Wullimann et al., 1991]. Labeled cells were also present in the torus semicircularis and in a brainstem nucleus located immediately lateral to the fourth ventricle and dorsal to the locus coeruleus (fig. 3e). We identify this brainstem nucleus as a putative secondary gustatory nucleus. It is not likely that the torus semicircularis and the putative secondary gustatory nucleus do project to the dorsal preglomerular nucleus, because both nuclei in other teleost species are known to have ascending projections to other preglomerular nuclei lying near the application site [Echteler, 1984; Murakami et al., 1986; Wullimann, 1988]. More importantly, after DiI application to the torus semicircularis in *Pantodon*, the dorsal preglomerular nucleus remains absolutely free of labeled terminals [M.F. Wullimann, unpubl. observ.]. Further, the connection from the periventricular nucleus of the lateral recess of the inferior lobe is almost certainly due to interruption of fibers projecting to the ventral preglomerular nucleus [M.F. Wullimann, unpubl. observ.].

There is little doubt, however, that the dorsal preglomerular nucleus of *Pantodon* receives afferents from the telenkephalon and has efferents to corpus cerebelli and torus longitudinalis, because we have established these connections both anterogradely and retrogradely. Also, dorsal preglomerular nuclei on both sides of the brain are undoubtedly reciprocally connected. This strongly implies that the dorsal preglomerular nucleus, unlike other preglomerular nuclei, lacks ascending projections and is exclusively involved in descending circuitry.

Similar interpretational problems exist with some connections reported after DiI application to the torus longitudinalis. The solely contralaterally labeled neurons in the torus semicircularis and the perilemniscal nucleus likely are due to labeling of fibers of passage that run via the intertectal commissure to terminate in the ablated tectum ipsilateral to the DiI application site in the torus longitudinalis (fig. 6a, b). This ablation prevented DiI transport via the ipsilateral tectum and explains the absence of ipsilaterally labeled neurons in the torus semicircularis and the perilemniscal nucleus. However, the anterograde label present in the deep white and the central zones of the contralateral tectum might originate in the torus semicircularis or perilemniscal nucleus ipsilateral to the DiI application site, since the anterograde transport within this pathway was not prevented by the ablation. The torus semicircularis indeed is bilaterally

labeled after HRP-injections into the tectum in *Pantodon* [M.F. Wullimann, unpubl. observ.].

If the anterograde label in the contralateral torus semicircularis and mesencephalic reticular formation originated in the (ablated) tectum of the other brain side, labeled neurons were – for reasons of symmetry – to be expected in the contralateral tectum. Since this is not the case, the said anterograde label might originate in the ipsilateral torus semicircularis.

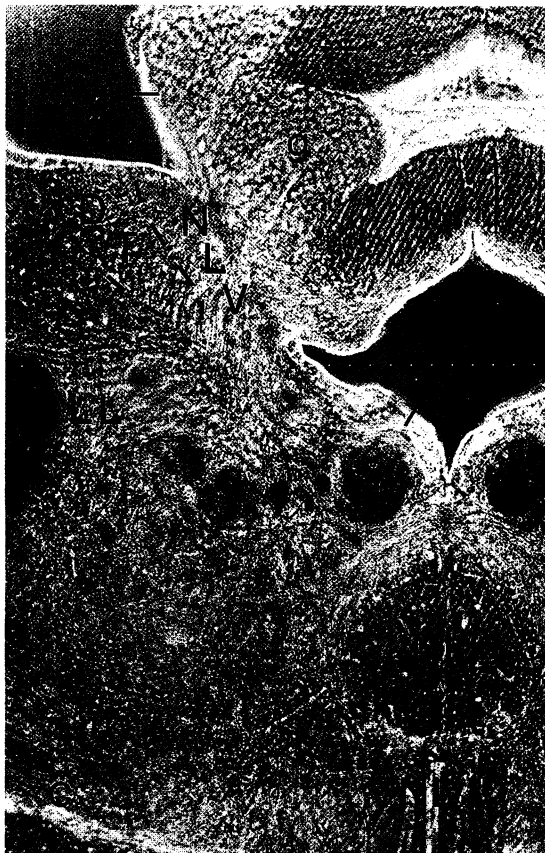
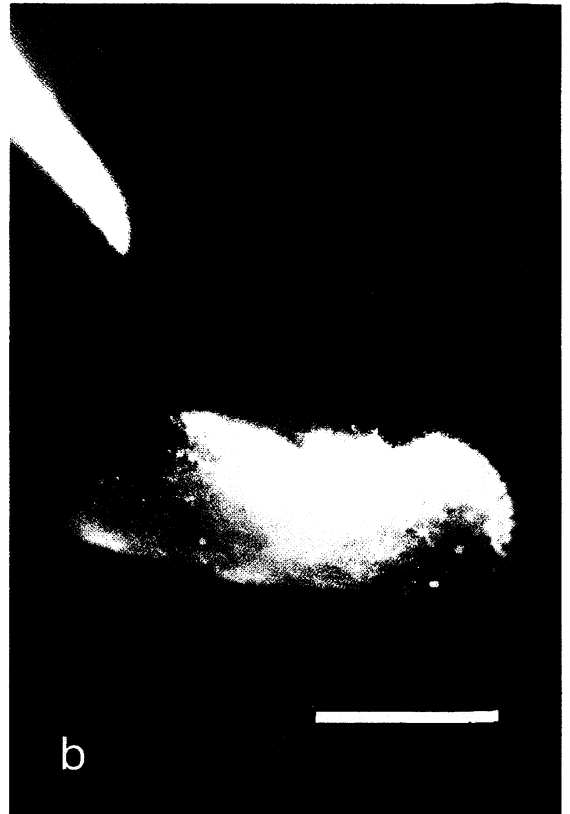
The terminal field in the corpus cerebelli seen following DiI application to the torus longitudinalis is very similar to that seen after DiI is applied to the dorsal preglomerular nucleus and likely represents labeling of collaterals. The sparse bilaterally labeled cells in Dc probably project to the ablated optic tectum.

The following would therefore appear to be the remaining connections of the torus longitudinalis: afferents from the contralateral ventral layer of the torus longitudinalis, bilateral afferents from the dorsal preglomerular and dorsal tegmental nuclei and from nucleus lateralis valvulae and oculomotor neurons; efferents to the contralateral intermediate layer of the torus longitudinalis, ipsilateral efferents to the marginal layer of the tectum, and bilateral efferents to nucleus interpeduncularis. The massive terminal field in nucleus interpeduncularis could, however, also be due to labeling of collaterals of retrogradely labeled neurons.

Functional Considerations

The torus longitudinalis is unique to actinopterygians, except for the polypteriforms, and has been functionally related to saccadic eye movements (dorsal portion) and to responses to dimming of the visual field (ventral portion) in several teleost species [Northmore et al., 1983; Northmore, 1984]. The input from the oculomotor neurons demonstrated in *Pantodon* may represent an efference copy to the torus longitudinalis during performance of saccadic eye movements and likely occurs in all teleosts. The sensory

Fig. 7. Photomicrographs of transverse sections through the brain of *Pantodon* showing: **a, b** retrogradely labeled neurons in the ipsilateral dorsal preglomerular nucleus after DiI application to the torus longitudinalis and **c, d** retrogradely labeled neurons contralaterally in the oculomotor area (large arrow), dorsal tegmental nucleus (DT), and nucleus lateralis valvulae (NLV), as well as a terminal field in the dorsal part of nucleus interpeduncularis. Note that some labeled fibers (probably representing collaterals of neurons in DT and/or NLV) enter the granular layer of the valvula cerebelli (small arrows). Sections in **b** and **d** are shown in phase contrast in **a** and **c**, respectively, to allow localization of labeled structures. For abbreviations see list. Bar in **b** = 0.1 mm for **a** and **b**; bar in **d** = 0.1 mm for **c** and **d**.



visual input related to the dimming response may come from nucleus lateralis valvulae (see below).

Here, we present the first demonstration that the torus longitudinalis of a teleost is mainly involved in descending telencephalic circuitry. The first three segments of this descending pathway are demonstrated in the present study with DiI: the central zone of area dorsalis telencephali to the dorsal preglomerular nucleus (PGd); PGd to the torus longitudinalis (TL), and TL to the optic tectum. The Dc has been interpreted as a composite telencephalic nucleus comprising the major efferent neurons of the dorsal telencephalic subdivisions [Northcutt, 1981]. In all teleosts that have been examined, the torus longitudinalis projects to the marginal layer of the ipsilateral optic tectum, as demonstrated here in *Pantodon*. Toral neurons projecting to the tectum are located exclusively within the intermediate layer of the torus longitudinalis [M.F. Wullimann, unpubl. observ. of HRP-material], which is the recipient zone of projections from the dorsal preglomerular nucleus. The optic tectum in turn is known to project heavily to brainstem nuclei in all vertebrates. Thus, the torus longitudinalis in *Pantodon* is one link of a multisynaptic – presumably premotor – pathway descending from the telencephalon to the brainstem. This pathway, via the dorsal preglomerular nucleus, may be uniquely derived (autapomorphic) for *Pantodon* (see Evolutionary Considerations).

Additional afferent sources of the torus longitudinalis in *Pantodon* originate bilaterally in the nucleus lateralis valvulae and dorsal tegmental nucleus but not in the valvula cerebelli. Based on degeneration and HRP-tracing, Ito and Kishida [1978] reported that the major (bilateral) input to the torus longitudinalis originates in the ipsilateral valvula in the carp *Cyprinus carpio*. The valvulo-toral fibers were reported to ascend through the ipsilateral tectum before entering the torus longitudinalis bilaterally [Ito and Kishida, 1978]. This pathway would appear to have been largely interrupted for ipsilateral DiI transport by our tectal ablation. However, labeled neurons in the contralateral valvula were to be expected also in our experiments.

Paradoxically, Ito and Yoshimoto [1990] reported recently – again based on HRP tracing in the same species – that ‘no labeled cells were found in the valvula cerebelli’ after injections of the torus longitudinalis, but they did report retrogradely labeled cells in a nucleus ventral to nucleus lateralis valvulae. This is very similar to our results in *Pantodon*, and the nucleus in *Cyprinus* likely corresponds to our dorsal tegmental nucleus in *Pantodon*. Since the dorsal tegmental nucleus and the nucleus lateralis valvulae are known to project to the valvula in two other teleost species [Wullimann and Northcutt, 1989], and since we

found labeled fibers in the granular layer of the valvula in *Pantodon*, it is very likely that the dorsal tegmental nucleus projects with collaterals both to the valvula and the torus longitudinalis in *Pantodon* and in other teleosts. Thus, tracer injections into the valvula might lead to a false positive result of an efferent projection to the torus longitudinalis.

The dorsal tegmental nucleus receives descending telencephalic input in *Pantodon* [M.F. Wullimann, unpubl. observ.], whereas nucleus lateralis valvulae receives inputs descending from the hypothalamus and ventral thalamus [Ito and Yoshimoto, 1990], the latter being a primary visual target.

Thus, the circuitry of the torus longitudinalis in *Pantodon* is rather simple: four inputs (dorsal preglomerular and dorsal tegmental nuclei plus nucleus lateralis valvulae and oculomotor neurons), and two outputs, one to the optic tectum and one to the nucleus interpeduncularis. Whereas the dorsal preglomerular nucleus may be autapomorphic for *Pantodon* (see Evolutionary Considerations), the remaining three input nuclei are ubiquitously present in teleosts. Oculomotor neurons likely provide an efference copy of oculomotor commands, and nucleus lateralis valvula and the dorsal tegmental nucleus likely relay diencephalic and telencephalic projections, respectively, to the torus longitudinalis. It can therefore be hypothesized that this neural organ, peculiar to teleosts, arose within the context of conveying forebrain commands multisynaptically to the tectum.

Similar to our report, Braford et al. [1992] describe in a recent abstract that the torus longitudinalis receives input from two dorsal tegmental nuclei in the osteoglossomorph *Xenomystus nigri*. In contrast to our results in *Pantodon*, these authors report an efferent, not an afferent, connection with a caudal preglomerular nucleus.

The dorsal preglomerular nucleus in *Pantodon* is also involved in a parallel telencephalic descending pathway to the corpus cerebelli. This is of particular interest phylogenetically (see below), because the electroreceptive mormyrids show similar circuitry.

Evolutionary Considerations

Gould and Vrba [1982] noted that an important term and, therefore, the concept behind it, is missing in the vocabulary of evolutionary biologists: exaptation. Any given biological structure or organ that fits its environment is aptive, but not necessarily adaptive. For being adaptive, a structure must have been selected in the first place by the environment to which it presently fits, i.e., the relationship between the two must be causal. Many structures do not

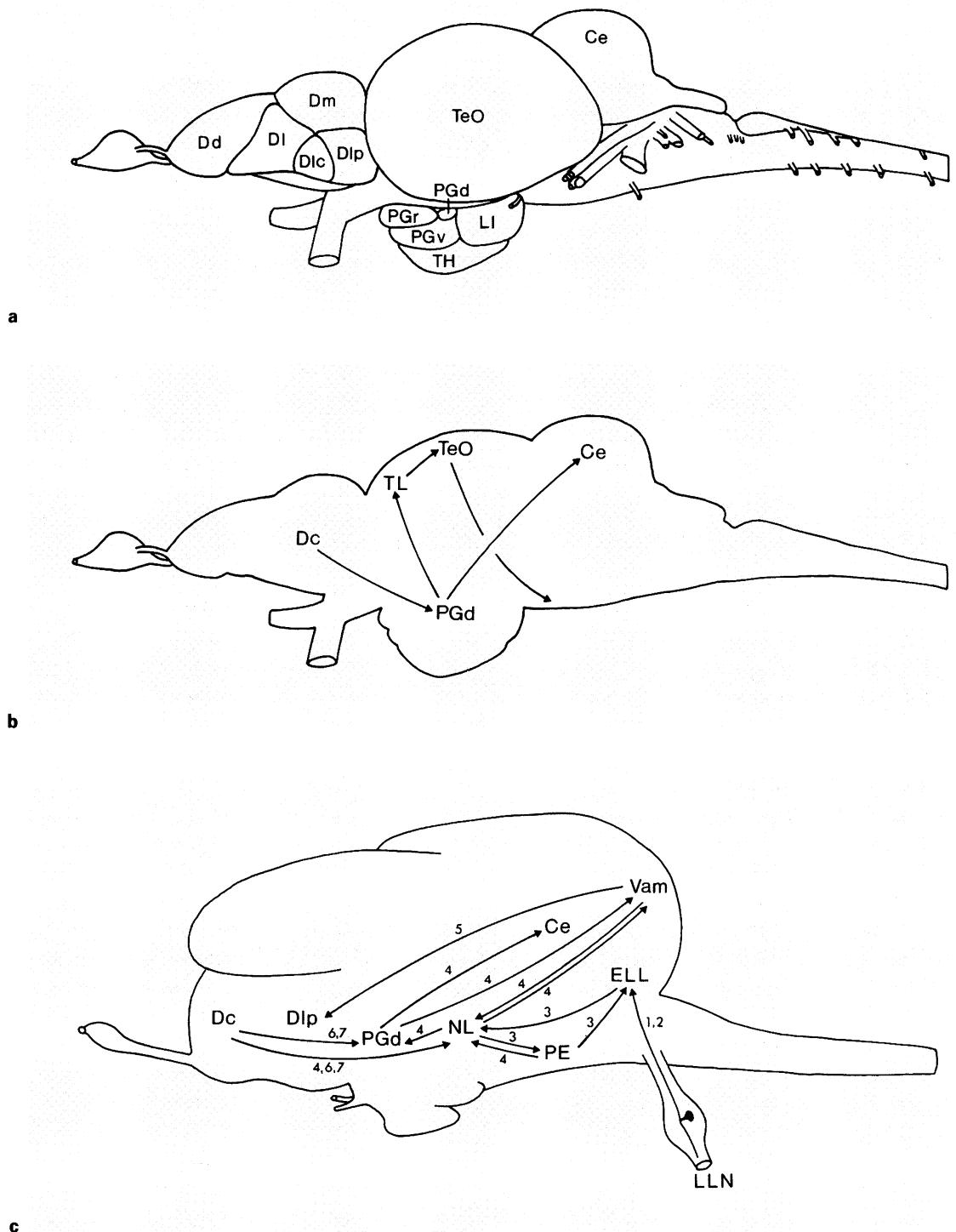


Fig. 8. Summary diagrams showing: **a** a lateral view of the brain of *Pantodon*, **b** the known circuitry of the dorsal preglomerular nucleus in this non-electroreceptive osteoglossomorph species, and **c** the circuitry in the electroreceptive *Gnathonemus*. Note the existence of a telencephalo-cerebellar pathway via the dorsal preglomerular nucleus in both species. Connections shown for *Gnathonemus* (**c**) were established by several researchers: 1: Bell and Russell, 1978; 2: Bell, 1981; 3: Bell et al., 1981; 4: Finger et al., 1981; 5: Haugedé-Carré, 1980; Wullimann and Rooney, 1990; 6: D.J. Rooney, pers. commun.; 7: Wullimann and Northcutt, 1990.

fulfill this requirement. The forelimbs of penguins certainly did not originate for aquatic locomotion; they are wings that have been secondarily altered during evolution for swimming. Pectoral fins of fishes, on the other hand, very likely developed for aquatic locomotion originally, i.e., they are adaptive. Penguin 'wings', however are exaptive. Logically then, the wings of the penguin's flying ancestors were preaptive [term coined by Gould and Vrba, 1982].

Only in cases where the history of a certain structure and of its function(s) is sufficiently known (as in the penguin example), are we able to distinguish between adaptation and exaptation. This rarely applies to CNS structures, since more often than not the function and systematic distribution of neural characters are unknown. However, electroreception and its related CNS circuitry is a fortunate exception. Although this sensory modality is plesiomorphic for vertebrates [Bullock et al., 1983], it was lost early in the evolution of ray-finned fishes and re-evolved several times independently in various teleost groups (e.g. mormyrids, gymnotoids).

The ascending lateral line mechanosensory pathway in actinopterygians runs from the primary sensory brainstem center to the torus semicircularis and from there to a laterally migrated portion of the posterior tuberculum (preglomerular complex of teleosts), which in turn acts as a relay station to the telencephalon [Murakami et al., 1983, 1986; McCormick, 1989; Wullimann and Northcutt, 1990; Striedter, 1990, 1991]. This pattern is plesiomorphic for actinopterygians, if not gnathostomes.

The electrolocative component of the electrosensory pathway in mormyrids is relayed in a way strikingly similar to that of the mechanosensory information. A parallel pathway via the electrosensory lateral line lobe, the lateral nucleus of the torus semicircularis, and the dorsal preglomerular nucleus has been described (for references see fig. 8c and Introduction). However, instead of being relayed directly from the preglomerular complex to the telencephalon, as is the case for mechanoreception, the electrolocative information reaches the dorsal preglomerular nucleus, which in turn projects to the medial leaf of the valvula [the mormyromast-ampullary region of Finger et al., 1981] and to the corpus cerebelli [Meek et al., 1986]. The dorsal preglomerular nucleus also receives a strong input from the telencephalon [Wullimann and Northcutt, 1987, 1990]. The medial leaf of the valvula in turn projects to the telencephalon [Haugedé-Carré, 1980; Wullimann and Rooney, 1990].

All of the central nervous electrosensory circuitry in mormyrids is, by definition, apomorphic, since the electro-sense evolved anew in this teleost group. This is particu-

larly evident for the cerebellar and telencephalic circuitry of the dorsal preglomerular nucleus, because similar connections have not been reported for any preglomerular nucleus in other teleosts outside the osteoglossomorphs [Wullimann and Northcutt, 1987, 1990]. Consequently, Wullimann and Northcutt [1987, 1990] interpreted the telencephalic and cerebellar connections of the dorsal preglomerular nucleus in *Gnathonemus* as an autapomorphy that arose in conjunction with the re-development of electroreception in mormyrids.

Surprisingly, in the present study we found that the non-electroreceptive *Pantodon* has a dorsal preglomerular nucleus which shares some similarities in connectivity with the comparable nucleus in *Gnathonemus*. In both species, the said nucleus receives a massive terminal field from Dc and projects to the corpus cerebelli (fig. 8). Interestingly, there is no projection to the valvula in *Pantodon*, in contrast to *Gnathonemus*. Furthermore, after DiI deposition to the posterior part of area dorsalis telencephali (Dlp) and long-term incubation (100 days), no retrogradely labeled eurydendroid cells were present in the corpus or the valvula cerebelli; i.e., *Pantodon* lacks the cerebello-telencephalic projection seen in *Gnathonemus* [Wullimann and Rooney, 1990].

The connections of the dorsal preglomerular nucleus in *Pantodon* are its telencephalic input and its descending output to two efferent targets, the corpus cerebelli and the torus longitudinalis (see Functional Considerations). This is in contrast to what has been reported for other preglomerular nuclei, which are always ascending relay nuclei of sensory systems [Northcutt and Wullimann, 1988; Wullimann and Northcutt, 1990]. Thus, the dorsal preglomerular nucleus in *Pantodon* clearly represents the descending link within the preglomerular area. If the dorsal preglomerular nucleus' projection to the corpus cerebelli seen in *Pantodon* is plesiomorphic for osteoglossomorphs, it may have represented a 'blueprint' for the additional development of a projection to the valvula in *Gnathonemus*. While the projection of the dorsal preglomerular nucleus to the corpus cerebelli in *Pantodon* cannot be involved in electroreception, the preglomerulo-cerebellar circuitry in *Gnathonemus* likely is and may therefore represent a case of neural exaptation. Critical to this interpretation is whether or not additional osteoglossomorphs have telencephalo-cerebellar circuitry via a dorsal preglomerular nucleus, i.e., whether or not this circuitry is homologous among osteoglossomorphs.

At this point of analysis, an alternative interpretation must be considered. The visual system in *Pantodon* [Butler and Sidel, 1991] is reduced in a similar way, albeit not to the same degree, as in *Gnathonemus*. The retinorecipient

parvocellular superficial pretectal nucleus is small and not pleated in *Pantodon* [Butler and Saidel, 1991] and is entirely absent in *Gnathonemus* [Wullimann and Northcutt, 1990]. The parvocellular superficial pretectal nucleus is also not pleated, if present at all, in notoptyrids [M.F. Wullimann, unpubl. observ.]. This is in contrast to the South American osteoglossomorphs *Osteoglossum* [Wullimann et al., 1991] and *Arapaima* [M.F. Wullimann, unpubl. observ.], where the parvocellular superficial pretectal nucleus is a large and pleated nucleus, a condition that has been concluded to be plesiomorphic for teleosts [Northcutt and Wullimann, 1988]. Thus, the following highly hypothetical scenario might apply to Old World osteoglossomorphs: an unknown external process may have led to the reduction of the visual system in Old World osteoglossomorphs, which effected at the same time – e.g. for developmental or other internal organismal reasons [Roth and Wake, 1989; Wake and Roth, 1989] – the establishment of the above described circuitry in *Pantodon* and *Gnathonemus* independently. Subsequently, both species may have incorporated this neuronal hardware into different functional contexts. Logically, the apparent similarity of the circuitry between *Pantodon*

and *Gnathonemus* is then to be interpreted as homoplasious and may be due to the genome having reacted in a comparable fashion to a reorganization of the brain.

The African osteoglossomorph fish *Heterotis niloticus* might provide a test for the ‘genome’-hypothesis just discussed. This fish has a highly hypertrophied gustatory system; i.e., the vagal lobes are very large and form a spiral [Braford, 1986]. It is not known whether or not the hypertrophy of the gustatory system is correlated with a reduction of the visual system in *Heterotis*. If so, one would – in accordance with the ‘genome’-hypothesis – expect to find a dorsal preglomerular nucleus homoplasious to the one in *Pantodon* and *Gnathonemus*.

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