

European Journal of Morphology

Formerly: Acta Morphologica Neerlandico-Scandinavica

182-50

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The Teleostean Torus Longitudinalis: A Short Review on its Structure, Histochemistry, Connectivity, Possible Function and Phylogeny

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ABSTRACT

The older idea that the torus longitudinalis (TL) is part of the ascending cerebellotectal circuitry involved in control of eye movements is at odds with facts on the histological, hodological and physiological level. Instead of an input from the valvula cerebelli, the TL and the cerebellum both receive a collateral mossy fiber input from the same source (nucleus lateralis valvulae, dorsal tegmental nucleus). The new hodological information is more consistent with fine histological and physiological data and suggests that the TL is a link in premotor circuitry descending from telencephalon to brain stem.

KEY WORDS: cerebellum - premotor circuitry - saccadic eye movement - telencephalon - torus longitudinalis

INTRODUCTION

The torus longitudinalis (TL) is a cigar-shaped, paired neural organ extending rostrocaudally immediately ventrally to the midline of the mesencephalic tectum (Fig. 1). The TL is present in all ray-finned fishes (actinopterygians) except in the polypteriforms and is absent in all other vertebrates (Nieuwenhuys & Pouwels, 1983). Therefore, the TL clearly represents a shared derived character (synapomorphy) uniting the actinopterygians. This fact deserves special attention by evolutionary neurobiologists, because it is very rare that a qualitatively entirely novel neural structure evolves in vertebrates. Here, our present knowledge on the torus longitudinalis' structure and histochemistry, its afferent and efferent connections and its attributed functions will be reviewed.

MORPHOLOGY AND HISTOLOGY

The TL is composed of relatively small, tightly packed and round neuronal perikarya which closely resemble cerebellar granular cells (Ito, 1971; Nieuwenhuys & Pouwels, 1983; Meek, 1992). The unmyelinated axons of the ipsilateral TL neurons extend mediolaterally into the most superficial part of the mesencephalic tectum, thus forming its

marginal layer (Fig. 1). Here, the TL axons contact along their course many perpendicular dendritic arbors of deep tectal neurons (Meek, 1990). This is somewhat comparable to the cytoarchitectonic interaction of cerebellar parallel fibers with the dendritic tree of Purkinje cells. Moreover, the TL receives glomerular synaptic endings typical for cerebellar mossy fiber endings (Ito, 1971). The size and distribution of cells within the TL need not be uniform. Ito (1971) described three cell size classes in the TL of the carp, *Cyprinus carpio*, and in the freshwater butterfly fish, *Pantodon buchholzi*, three dorsoventrally arranged layers can be recognized in the TL based on the differential clustering of cells (Wullimann & Roth, 1994).

CONNECTIVITY

Exclusively hodological data gained with tract-tracing techniques (silver degeneration, horseradish peroxidase, fluorescent tracers) will be considered here (see Table 1).

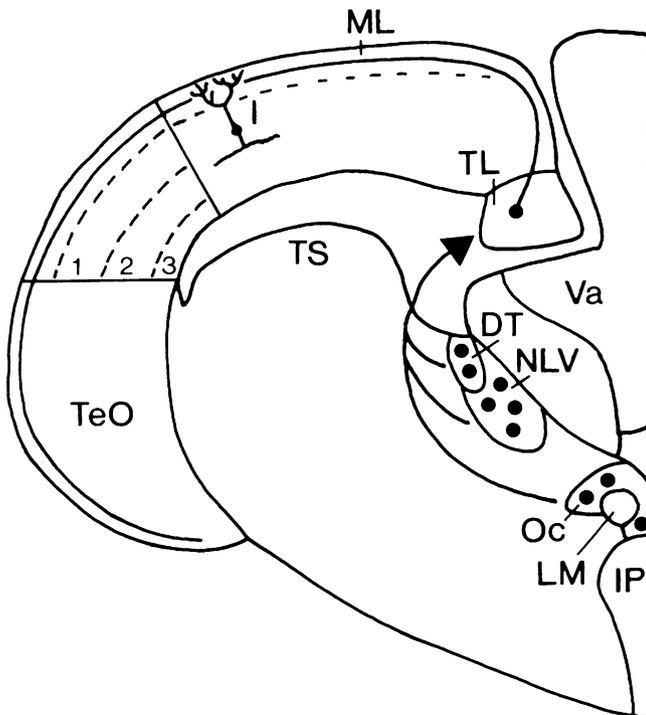
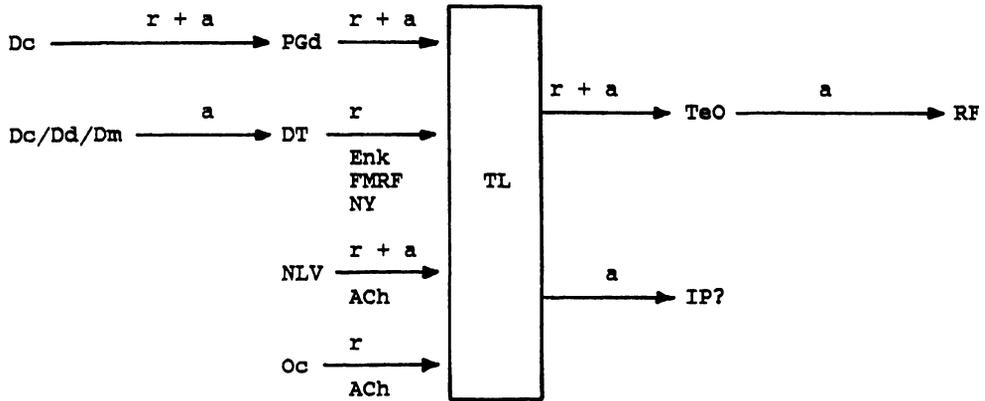


Fig. 1. The afferent and efferent organization of the teleostean torus longitudinalis in a semischematic diagram. Only connections representing the likely ancestral condition for teleosts are included (see text). Abbreviations and numbers: 1: superficial gray and white tectal zone, 2: central gray tectal zone (including deep white zone), 3: periventricular gray tectal zone, DT: dorsal tegmental nucleus, I: type I interneuron, IP: interpeduncular nucleus, LM: medial longitudinal fascicle, ML: marginal tectal layer, NLV: nucleus lateralis valvulae, Oc: oculomotor neurons, TeO: optic tectum, TL: longitudinal torus, TS: torus semicircularis, Va: valvula cerebelli.

Table 1. Connections of the torus longitudinalis established with modern neuronal tracer techniques (a: anterogradely, r: retrogradely) and possible neuroactive substances involved (ACh: acetylcholine, Enk: enkephalin, FMRF: F<RF-amide, NY: neuropeptide Y). Abbreviations for nuclei: Dc, Dd, Dm: Central, dorsal and medial divisions of area dorsalis telencephali, DT: dorsal tegmental nucleus, IP: interpeduncular nucleus, NLV: nucleus lateralis valvulae, Oc: oculomotor neurons, PGd: dorsal preglomerular nucleus, RF: reticular formation, TeO: optic tectum, TL: longitudinal torus. For citations see text.

TELENCEPHALON DIENCEPHALON/MESENCEPHALON MEDULLA OBLONGATA



Afferent connections

Anterograde tracer experiments in the carp, *Cyprinus carpio*, indicated that the TL receives a bilateral afferent projection from the valvula cerebelli (Ito & Kishida, 1978). Therefore, until recently it was generally accepted that the TL is part of a cerebellotectal circuit. However, Ito & Yoshimoto (1990) later reported, again in the carp, that the neurons labeled retrogradely from the TL are located outside of the valvula cerebelli, ventral to it. Further, these authors established anterogradely that the nucleus lateralis valvulae projects bilaterally to the TL. This is in agreement with data on retrogradely established inputs to the TL in *Pantodon buchholzi* (Wullimann & Roth, 1994), where no labeled cells were found in any part of the cerebellum, but instead neurons in the dorsal tegmental nucleus and in the nucleus lateralis valvulae were labeled bilaterally.

The latter nuclei are the major sources of mossy fiber input to the cerebellum (Finger, 1978; Meek et al., 1986; Wullimann & Northcutt, 1988, 1989). Thus, neurons in these two nuclei likely project with collaterals to both the granular layer of the whole cerebellum **and** the TL. This interpretation is beautifully consistent with the observation of mossy fiber-like glomerular endings in the carp TL (Ito, 1971), and further explains why terminals are seen in the TL after tracer application not only to the valvula cerebelli (Ito & Kishida, 1978) but also to the corpus cerebelli (Wullimann & Northcutt, 1988).

The dorsal tegmental nucleus receives a telencephalic input in various teleost species (*Sebastiscus marmoratus*: Murakami et al., 1983; *Gnathonemus petersii*: Wullimann & Northcutt, 1990; *Carassius auratus*: Wullimann & Meyer, 1993). Further, the nucleus lateralis valvulae of the carp (Ito & Yoshimoto, 1990) receives input from the (gustatory-related) hypothalamic inferior lobe, from the ventral thalamus and from the magnocellular pretectal nucleus (both visually-related).

Additional inputs to the TL of *Pantodon* were reported to originate in the ventral layer of the contralateral TL, bilaterally in oculomotor neurons of either the oculomotor or trochlear nuclei and, bilaterally, in a nucleus of the preglomerular complex (Wullimann & Roth, 1994). Whereas the first two inputs to the TL likely are general teleostean characters, the input from the telencephalo-recipient dorsal preglomerular nucleus appears to be an uniquely derived feature of osteoglossomorph teleosts (extensively discussed in Wullimann & Roth, 1994).

Efferent connections

In all teleosts examined, the axons of TL neurons project tangentially into the ipsilateral marginal layer of the mesencephalic tectum (Ito & Kishida, 1978; Grover & Sharma, 1981; Luiten, 1981). In *Pantodon buchholzi*, these neurons are restricted to the intermediate layer of the TL (Wullimann & Roth, 1994). Within the tectal marginal layer, the TL axons contact all along their course the dendritic trees of many neuronal perikarya located in the tectal superficial grey and white zone (type I tectal interneurons; Meek, 1981). The type I interneurons receive additional, primary retinal input close to the perikaryon, and have a basal dendritic shaft in the central grey zone colocalized with direct telencephalic input to the tectum. Further, the type I interneurons are said to contact in turn several types of efferent tectal cells (types X, XII, XIII, XIV), two of which (types XII and XIII) project to the rhombencephalic reticular formation (Meek, 1990).

A possible second efferent connection of the TL was suggested to reach bilaterally the dorsal interpeduncular nucleus in *Pantodon buchholzi* (Wullimann & Roth, 1994). However, this connection was established only anterogradely. The terminals in the interpeduncular nucleus may, therefore, represent labeled collaterals of neurons projecting to the TL, e.g. of neurons in the dorsal tegmental nucleus. Interestingly, the area dorsalis tegmentalis of mammals is not only known to provide an input to the interpeduncular nucleus (Briggs & Kaelber, 1971; Marchand et al., 1980; Contestabile & Flumerfelt, 1981), but it further resembles the dorsal tegmental nucleus of teleosts in that it receives a telencephalic input (Nieuwenhuys et al., 1988).

In summary

It can be stated that the TL (1) is part of multisynaptic neuronal circuitry from telencephalon to brain stem, (2) receives direct input from oculomotor neurons, and (3) is part of higher order sensory circuitry involving the hypothalamus, ventral thalamus and pretectum.

HISTOCHEMISTRY

In contrast to stained fibers and terminals revealed by various (immuno-)histochemical studies in the torus longitudinalis, stained perikarya were not reported in the TL. Thus, putative efferent neurotransmitters/neuromodulators of the TL remain unknown. However, the evidence regarding neuroactive substances involved with afferents to the TL can, in some cases, reasonably be related to possible neuronal sources in nuclei afferent to the TL mentioned above (see Table 1).

Acetylcholine. Choline acetyltransferase immunoreactive (ir) fibers – although not reported in the TL of the minnow, *Phoxinus phoxinus* (Ekström, 1987) – are present in the TL of the European eel, *Anguilla anguilla* (Molist et al., 1993). In the latter species

these fibers may originate in (cholinergic) oculomotor neurons. However, in both species, cholinergic neurons have also been reported in the nucleus lateralis valvulae, which is one of the reported inputs to the TL.

Monoamines. Serotonergic fibers in the TL were reported immunohistochemically in the goldfish, *Carassius auratus* (Kah & Chambolle, 1983). This is in surprising contrast to the absence of such immunoreactivity in three other teleost species, namely the mormyrid *Gnathonemus petersii* (Meek & Joosten, 1989), the silurid *Clarias gariepinus* (Corio et al., 1991) and the stickleback, *Gasterosteus aculeatus* (Ekström & van Veen, 1984), since profuse serotonergic innervation of the adjacent tectum was noted in all three species mentioned. None of the serotonergic nuclei indicated in the goldfish (Kah & Chambolle, 1983) appears to represent one of the afferent nuclei to the TL described above. Thus, a serotonergic input to the TL may be unique to some teleosts such as the goldfish. There is some immunohistochemical evidence for a scant dopaminergic innervation of the TL in *Carassius auratus* (tyrosine hydroxylase; Hornby et al., 1987) and in *Gasterosteus aculeatus* (dopamine; Ekström et al., 1990). However, its neuronal origin remains elusive.

Aminoacids. One of three subtypes of kainate binding sites is only found in the TL (and in the cerebellar molecular layer) of *Telapilia monsanbica* (Tong et al., 1992). Although kainate is an analogue of L-glutamate, the physiological role of the said binding site and its relationship to amino-acids remains unclear.

Neuropeptides. Antibodies against the molluscan cardioexcitatory tetrapeptide FMRF-amide revealed stained fibers in the TL of *Carassius auratus* (Bonn & König, 1989) and the green molly, *Poecilia latipinna* (Batten et al., 1990). These fibers may originate in the ganglion cells of the terminal nerve. More consistent with the hodological data is the hypothesis that they may stem from the dorsal tegmental nucleus, since neurons in this area have been reported to contain FMRF-amide (Batten et al., 1990; 'laminar nucleus' of Vecino & Ekström, 1992). Enkephalinergetic fibers in the TL and perikarya in the dorsal tegmental area were reported in *Poecilia latipinna* (Batten et al., 1990) suggesting that at least part of the projection from the dorsal tegmental nucleus to the TL may be enkephalinergetic in teleosts. Neuropeptide Y-immunoreactive fibers occur in the TL of the atlantic salmon, *Salmo salar* (Vecino & Ekström, 1990). They may originate in the salmon's 'laminar nucleus' of Vecino & Ekström (1992) since these neurons are NY-ir and may be part of the dorsal tegmental nucleus. *Poecilia latipinna* was also reported to have NY-ir neurons in the dorsal tegmental area (Batten et al., 1990).

PHYSIOLOGY AND FUNCTION

Electrophysiological experiments were carried out in a set-up mimicking the natural stimulus propagation from TL to tectal neurons in two percomorph teleosts (*Eugerres*, *Holocentrus*; Vanegas et al., 1979). Electrical stimulation of fibers in the tectal marginal layer and recording of the resulting field potential at different depths and mediolateral locations in the tectum demonstrates the electrical activity of the involved presynaptic (TL-axon) and postsynaptic (type I tectal interneuron) neuronal elements. The spatio-temporal characteristics of the multiple waves constituting this field potential reveal close similarity to the electrical propagation in pre- and postsynaptic elements in the cerebellar parallel fiber/Purkyně cell system (Vanegas et al., 1979). In that study, it was further noted that there must be two classes of TL axons judged from the existence of two

distinct propagation velocities. This particular fact was used by Meek (1992) to suggest an elaborated model how the teleostean TL-optic tectum system might perform coincidence detection.

Recordings of multiunit activity in the TL of two marine teleosts (*Eugerres plumieri*, *Holocentrus ascencionis*; Northmore et al., 1983) and of the goldfish (Northmore, 1984) revealed unequivocally that dorsally located TL neurons respond with a sustained discharge to visual stimuli (i.e. dimming of contralateral visual field) and that ventrally located TL neurons give bursts of activity accompanying spontaneous saccadic eye movements. The latter bursts in the TL occurred in response to active, but not passive, eye movement and persisted in the dark and after paralysis. This indicates that the bursts neither depend directly upon visual nor proprioceptive input, but rather depend upon a central motor corollary discharge to the TL. Because the saccade-related bursts in the TL were abolished by intersection or ablation of the valvula cerebelli, Northmore (1984) assumed in consistency with the earlier hodological data that the valvula is the source of this corollary discharge to the TL. However, the trochlear nerve was reportedly also injured by the lesions to the valvula (Northmore, 1984) and may have caused the abolishment of the saccade-related bursts in the TL. This is consistent with new hodological data (Wullimann & Roth, 1994) that offer the most direct source for the said corollary discharge, i.e. an efference copy from oculomotor/trochlear neurons.

The photic response in the dorsal TL was concluded to depend upon an input from the ipsilateral optic tectum (Northmore et al., 1983, Northmore, 1984), partially because the ablation of the latter abolished this response. Consistent with the new hodological information (Wullimann & Roth, 1994), an alternative explanation exists: The tectorecipient magnocellular pretectal nucleus is a major input to nucleus lateralis valvulae (Northcutt & Braford, 1984; Ito & Yoshimoto, 1990) and ablation of the tectum may abolish the photic response in the TL via this multisynaptic pathway. The reported much longer latency of the response to a visual stimulus (15ms more after onset; 10ms more after offset) in the TL compared to the tectum is in support of this interpretation.

PHYLOGENY

What may be the reason for the phylogenetic development of a novel neural structure such as the TL? This structure clearly is an integral part of multisynaptically relayed descending telencephalic (presumably premotor) circuitry to the brainstem and receives in addition corollary oculomotor and sensory information. It may not be a coincidence that the few unambiguous examples for qualitatively new central nervous structures (such as pallio-spinal and pallio-pontine tracts in birds and mammals) also represent descending telencephalic circuitry. More detailed information of the physiological properties of this circuitry in teleosts holds the promise to reveal the function and biological role(s) of the TL at its phylogenetic inception.

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