Anterograde labelling from the optic nerve reveals multiple central targets in the teleost, *Lethrinus chrysostomus* (Perciformes)

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Summary. Cobaltous-lysine is transported anterogradely from the optic nerve of the teleost, *Lethrinus chrysostomus* (Lethrinidae, Perciformes). The marginal optic tract is labelled in longitudinal bands of light and dark staining fibres which persists caudally within the ventral division but not in the dorsal division. This species possesses multiple central targets in the contralateral preoptic, diencephalic, pretectal, periventricular and tectal regions of the brain. In addition, a greater subdivision of the marginal optic tract is found to project to various nuclei. Ipsilateral projections are found in the suprachiasmatic nucleus and in the region of the horizontal commissure. Projections are also found in the telencephalic region of the nucleus olfactoryretinalis and the thalamic region of the nucleus thalamoretinalis. The retinotopicity of some of these nuclei, found in previous studies, is discussed in relation to the possibility of specific sub-populations of retinal ganglion cells having different central targets.

Key words: Visual system – Retinal projections – Optic tectum – Pretectum – Cobalt filling – Teleost – *Lethrinus chrysostomus* (Teleostei)

Extensive studies of the topographic arrangement of cells within the ganglion cell layer of teleosts (Ito and Murakami

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Abbreviations used in the text and figures: *A* nucleus anterior-thalami; *AO* accessory optic nucleus; *AOT* accessory optic tract; *AxOT* axial optic tract; *BO* nucleus of the basal optic root; *C* cerebellum; *HCv* ventral division of horizontal commissure; *I* nucleus intermedius thalami; *IL* inferior lobe; *MdOT* medial optic tract; *MO* medulla oblongata; *MOTd* dorsal division of the marginal optic tract; *MOTi* intermediate division of the marginal optic tract; *MOTv* ventral division of the marginal optic tract; *O* olfactory bulb; *OT* optic tract; *PC* nucleus pretectalis centralis; *PCo* posterior commissure; *Pd* nucleus pretectalis dorsalis; *PG* preglomerular complex; *PPd* nucleus pretectalis periventricularis, pars dorsalis; *PPv* nucleus pretectalis periventricularis, pars ventralis; *PSm* nucleus pretectalis superficialis pars magnocellularis; *PSp* nucleus pretectalis superficialis, pars parvocellularis; *Sn* suprachiasmatic nucleus; *TEL* telencephalon; *TeO* optic tectum; *TL* torus longitudinalis; *TrOlfr* tractus olfactoryretinalis; *VCg* granular layer of the valvula cerebelli; *VM* nucleus medialis thalami; *VL* nucleus ventrolateralis thalami; *VMdOT* ventro-medial optic tract

1984; Collin and Pettigrew 1988a, b) has revealed a number of specializations, termed *areae centrales*, which lie in different retinal positions. Subsequent confirmation of the proportion of cells in the ganglion cell layer that possess an axon leaving the retina via the optic nerve has involved retrograde labelling from the optic nerve (Collin and Pettigrew 1988c) and reveals that the topography and peak cell densities within the *area centrales* are unchanged with the inclusion of the non-ganglion cell population. Morphological examination of these retrogradely-labelled cells also reveals a large variation and up to nine classes have been characterized on the basis of soma size and location, primary and secondary branching pattern, dendritic field size, orientation and dendritic termination areas (Collin 1988). The major finding is that the position of a number of morphologically-characterized ganglion cells varies with eccentricity. Ganglion cells, with small soma and restricted dendritic fields oriented away from the *area centralis*, predominate within regions of highest ganglion cell density in contrast to the remaining parts of the retina which possess larger cells with morphological differences in soma size, branching and orientation. Since the *area centralis* possesses the highest densities of ganglion cells and is thought to mediate higher visual acuity (Hughes 1977), could there be specific morphological subsets of ganglion cells in the teleost retina that subserve higher visual acuity as there are in primates (Leventhal et al. 1981), other mammals (Rowe and Dreher 1982a, b) and birds (Bravo and Pettigrew 1981)? In order to answer this question definitively, anterogradely-labelled, retino-recipient nuclei within the brain must then be retrogradely-labelled and each population of retinal ganglion cells characterized and their topography mapped in relation to the total population of ganglion cells.

As part of a larger study, anterograde labelling has been used to trace optic nerve axons to central targets in the brains of a large number of teleosts. The cobalt-lysine technique was employed since it is thought to be more sensitive than degeneration techniques (Sharma 1972; Reperant and Lemire 1976; Ebbesson and Ito 1980) and autoradiography (Neale et al. 1972; Landreth et al. 1975; Voneida and Sligar 1976), and is also contained within the optic axons. Other recent studies using horseradish peroxidase (HRP, Fraley and Sharma 1984; Fritzsche et al. 1987; Babu and Prasada Rao 1988) and cobalt-lysine (Presson et al. 1985; Springer and Mednick 1985) have concentrated on the retinofugal and retinopetal projections in cichlids and goldfish.

The aim of this study was to investigate the entire retinofugal projection pattern of the teleost *Lethrinus chrysostomus* which has undergone extensive topographic analysis of the retinal ganglion cell layer (Collin and Pettigrew 1988b). This will enable subsequent studies to label retinorecipient nuclei and the morphology of retrogradely-labelled ganglion cells assessed with respect to the functional organization of cells in the area centralis.

Materials and methods

Anterograde labelling with cobalt-lysine

Five adult specimens of the red-throated emperor *Lethrinus chrysostomus* (Lethrinidae, Perciformes), 250–360 mm in length, were captured and maintained at 24° C in a filtered and well aerated aquarium. All fish were anesthetized with tricaine methane sulphonate (MS 222, 1:10000) and placed on a wet platform so that anesthetic and sea water could be continuously passed over the gills via an oxygenation column. The right eye of each fish was rotated nasally and the extraocular muscles severed with care taken not to puncture the ophthalmic artery. This artery was either sutured or cauterized in order to stop any loss of blood. The right eye was then removed and the optic nerve carefully isolated. The nerve was drawn up by suction into a pre-fitted silicon tube which was held in place by paraffin wax. The tube was then filled with a cobaltous-lysine solution prepared according to Lazar (1978). Briefly, 1.76 g $\text{CoCl}_2 \cdot 6 \text{H}_2\text{O}$ and 3.59 g L-lysine base (Sigma L-5501) were dissolved in 12 ml H_2O by stirring for 24 h. The pH was adjusted to 7.2 with concentrated HCl and distilled water was added to bring the final volume to 20 ml and sealed with more paraffin wax. Each fish was allowed to recover in a constant temperature (24° C), well aerated aquarium. After 3 to 5 days, the fish were reanesthetized with MS222 (1:5000) and perfused transcardially with 100 ml of 0.25% ammonium sulphide in Millionig's phosphate buffer, pH 7.4. This was followed by 100 ml phosphate buffer and 100 ml 3% paraformaldehyde in phosphate buffer, pH 7.4.

After removal, the brains were then postfixed in 3% glutaraldehyde in phosphate buffer, pH 7.4 for 1 h and prepared for frozen sectioning. An egg-yolk embedding technique was developed to overcome the problems of mounting a multi-lobed teleost brain in the correct orientation. Egg yolk (10 ml) and sucrose (3 g) were mixed on a magnetic stirrer until dissolved. The brain was coated with this mixture and allowed to dry for 3 min. Concentrated glutaraldehyde (0.8 ml) was added to the egg yolk and this mixture poured into a paper mold containing the brain which was held in place with minution pins. The embedding mixture set in 5–10 s and the block was then trimmed in preparation for sectioning.

Frozen transverse sections (50 μm) were mounted and intensified using a slightly modified Gallyas (1979) procedure developed by Bazer and Ebbesson (1984). The intensification solution, which was used at room temperature and in the light, was prepared as follows. Stock solution A: 355 ml distilled water, 1.5 g sodium acetate $3 \text{H}_2\text{O}$, 30 ml glacial acetic acid and 0.5 g silver nitrate. These were mixed overnight, filtered and 15 ml 1% Triton X-100 added. Stock solution B: 50 ml 5% sodium tungstate (freshly prepared). Stock solution C: 50 ml 0.25% ascorbic acid (freshly prepared). Sections were intensified for between 6 and 12 min in two freshly prepared mixtures of 8 parts A, one part

B and one part C. Each section was washed in three changes of distilled water and the silver intensified projections toned with 0.5% gold chloride for 15 s. Toning was also used to reduce background staining. Three further washes of distilled water and 5 min in a 1% sodium thiosulphate solution preceded two more washes in distilled water. A one-in-two series of sections were counterstained in 0.5% cresyl violet for 2 min and all sections were then dehydrated, cleared and coverslipped in DPX.

Intensified sections were viewed and photographed on a Leitz Dialux 20 compound microscope with 32ASA Panatomic-X film using a blue filter. Drawings were made from tracings of selected sections using a Leitz projection microscope at a magnification of 16. The nomenclature follows that of Braford and Northcutt (1983) unless stated otherwise.

Results

The cobaltous-lysine technique provided an excellent method of tracing optic tracts with good resolution and allowed the paths of fine fibres to be followed for long distances. Retinal targets were recognized by the appearance of dense aggregations of fibres associated with small varicosities. In all experiments, tracing of the retinofugal projections from the entire optic nerve was attempted and their subsequent central targets in the diencephalon, pretectum and tectum investigated.

A list of all abbreviations used in this study is provided on the title page. Fig. 1 illustrates the approximate locations of each transverse section of the brain of *L. chrysostomus* presented alphabetically in Fig. 2.

Divisions of the main optic tract and their central termination areas

Axial optic tract. At the level of the suprachiasmatic nucleus, approximately 200 μm past the optic chiasm, the marginal optic tract (MOT) divided medially to form a distinct axial optic tract (AxOT). In *L. chrysostomus*, a number of these fibres coursed laterally and innervated the ventral region of the contralateral suprachiasmatic nucleus (Sn, Figs. 2D, E; 3A, B). A smaller number of fibres then recrossed across the horizontal commissure and innervated the ipsilateral suprachiasmatic nucleus. The remaining fibres continued dorsally and caudally and passed through the cellular fields of the nucleus preopticus parvocellularis posterioris with a few fibres reaching the rostral tuberal region. At the level of the pretectum, the axial optic tract rejoined the marginal optic tract via the nucleus of the basal optic root (BO). This nucleus divided into three dorso-ventrally oriented regions with a smaller medial region receiving dense labelling. It was not possible to determine whether any fibres of AxOT contributed to the medial optic tract or thalamic nuclei.

The ventro-medial optic tract (VMdOT). The projections of the ventro-medial optic tract (VMdOT) was complicated and it was not certain whether this tract was a continuation of the axial optic tract (AxOT) after it rejoined the marginal optic tract or a separate tract which projected from the ventral division of the marginal optic tract caudally.

The axial optic tract of *L. chrysostomus* may be synonymous with the fasciculus ventromedialis tractus opticus (FVMTrO) in *Haplochromis* (Presson et al. 1985) and *As-*

Fig. 1 A. Lateral view of the brain of the red-throated emperor, *Lethrinus chrysostomus*. C cerebellum; IL inferior lobe; MO medulla oblongata; O olfactory bulb; OT optic tract; TEL telencephalon; TeO optic tectum. **B** Lateral view of the brain of *L. chrysostomus* showing the plane of transverse sections (A–M) traced through Fig. 2. Scale bars = 3 mm

tronotus (Springer and Mednick 1985) and the fasciculus medialis tractus opticus (FMTrO) in *Carassius* (Fraley and Sharma 1984). However, the continuation of this tract, after it rejoins the marginal optic tract, will be called the ventro-medial optic tract (VMdOT) to differentiate it from the AxOT, in this study, due to its caudal position and relatively large number of fibres.

The VMdOT was evident within the preoptic area, where it projected abruptly latero-caudally and was only distinguished in the diencephalon by a fibre bundle which traversed deep within, and perpendicular to, the fibres of MOT. In the pretectum, it projected medio-dorsally and rostrally to cross the accessory optic tract (Fig. 2J). It was not possible, at the level of the light microscope, to differentiate these two fibre tracts as they crossed. However, VMdOT seemed to continue caudally and sent fibres to the nucleus pretectalis periventricularis pars ventralis (PPv), nucleus pretectalis periventricularis pars dorsalis (PPd), nucleus pretectalis dorsalis (Pd) and terminated within the deeper layers of the central zone of the ventrolateral optic tectum (TeO). More caudally, VMdOT seemed to terminate in a hypothalamic nucleus before arching rostrally to project into the pretectum (Fig. 2K).

Anders and Hibbard (1974) described a similar pathway to VMdOT of this study. In the preoptic area, their fasciculus medialis nervi optici (FMNO) could be considered homologous to AxOT but, after VMdOT rejoined the marginal optic tract, it separated caudally and continued dorsally and innervated a number of nuclei before terminating in the stratum album centrale of the tectum (deep white zone of this study).

Ventral division of the marginal optic tract (MOTv). At the chiasm, there was a total decussation of optic fibres which projected to the contralateral hemisphere. The marginal optic tract was labelled in longitudinal bands of light- and dark-stained fibres which persisted caudally within the ventral division (MOTv) (Figs. 2D, E; 3C) but not in the dorsal division (MOTd) (Fig. 2D, E). The subdivision into dorsal and ventral tracts arose in the superficial pretectum. However, just before this bifurcation, the MOT supplied a large number of fibres to the nucleus pretectalis superficialis pars parvocellularis (PSP, Figs. 2D–G; 4A). This nucle-

us was a large complex structure situated against the lateral wall of the brain, rostral of the optic tectum. Convoluted at least 11 times in transverse section, PSP appeared to be elongated rostrocaudally and received a large input from both MOT and, more caudally, fibres solely from MOTv. No retinal input was found within the magnocellular division of the superficial pretectal nucleus.

In the region of the ventral division of the horizontal commissure (HCv), a small number of faint projections, from the medial wall of MOTv, recrossed across the horizontal commissure as far as the nucleus lateralis hypothalamus (Fig. 2G). En passant a few fibres branched dorsally and projected to both the ipsi- and contralateral sides of the midline. No nucleus of the ventral optic tract was observed in this species.

Two other targets were innervated by MOTv. A large nucleus of the basal optic root (BO) received input from medio-dorsal fibres of MOTv and laterally-directed fibres from the axial optic tract (Fig. 2G). A number of dense fibre aggregations were labelled within this nucleus which was partly embedded within a third distinct intermediate division of MOT (MOTi, Fig. 2G). More caudally, a thick fascicle projected medially and innervated the accessory optic nucleus which was situated near the medial wall of the pretectum (Fig. 2J–L). No preglomerular nuclear complex was found.

Dorsally, MOTv and MOTi formed thick fascicles before supplying all of the superficial white and gray zone (SWGZ) within the optic tectum (Fig. 2G, H; 4B, C). However, more darkly-stained fibres appeared as four distinct layers and fibres from the outer layers possessed larger diameter axons. A single well-labelled fascicle also projected lateral of PSP and terminated in the superficial layer of SWGZ in the ventro-lateral optic tectum (Fig. 4B, C). In caudal tectum, a number of fibres crossed from SWGZ through the central zone to the deep white zone.

Dorsal division of the marginal optic tract (MOTd). The dorsal division of the marginal optic tract (MOTd) initially contributed a large input to PSP before it continued rostrocaudally and innervated the nucleus pretectalis centralis (PC) which was partly embedded within MOTd (Fig. 2G). Fibre bundles then projected rostro-dorsally as distinct fas-

Fig. 2. Series of transverse sections through the brain of *L. chrysotomus* tracing the cobalt-lysine stained retinofugal pathways and central terminations. Drawings were made using a projection microscope. Each selected section (50 μ m), labelled alphabetically A–M, is approximately located in the planes illustrated in Fig. 1. However, the exact distance from the rostral telencephalon for each section is as follows; A: 4.85 mm; B: 5.05 mm; C: 5.45 mm; D: 5.75 mm; E: 5.95 mm; F: 6.15 mm; G: 6.35 mm; H: 6.45 mm; I: 6.65 mm; J: 6.95 mm; K: 7.25 mm; L: 7.35 mm; M: 7.75 mm. Tracts are depicted as solid lines and terminals or putative termination areas by dots. Full descriptions of all abbreviations are outlined on the title page

cicles and terminated within the rostro-medial wall of the optic tectum. Fibres from thalamic nuclei also rejoined MOTd and terminated in the tectum.

Medial optic tract (MdOT). Optic innervation of the thalamus and optic tectum was provided by the medial optic tract (MdOT) which coursed medio-dorsally from MOT, just caudal of the optic chiasm. Retinofugal input via MdOT innervated three thalamic nuclei and a few fibres traversed a fourth nucleus. In rostral thalamus, the nucleus anterior thalami (A), the nucleus intermedius thalami (I) and a large rostro-caudally elongated nucleus ventrolateralis thalami (VL) were distinguished. A few fibres also pro-

jected medially to the ventricle wall from VL, but it is not certain whether these made any synaptic connections with the nucleus ventromedialis thalami (VM, Fig. 2E). Since no sagittal sections were made, it was not known whether fibres that innervated the thalamic nuclei also innervated the periventricular pretectal nuclei.

The component of optic fibres that continued into the optic tectum, first divided into dorsal and ventral fascicles at the level of the posterior commissure (PCo, Fig. 2H). The dorsal fascicles then projected into the deeper layers of the central and deep white zones in the dorso-medial optic tectum while the ventral fascicles projected into the deeper layers of the central and deep white zones in the ventro-lateral tectum (Fig. 2H, I).

Olfactoretinalis tract (TrOlfR). In the preoptic region just rostral of the suprachiasmatic nuclei, approximately 90 fibres joined MOT via AxOT from the ventral telencephalon (Fig. 2B, C). These labelled fibres persisted rostrally almost as far as the olfactory bulb before they disappeared. Although no retinopetal somata were found, it was assumed that the observed projections were efferent fibres from the nucleus olfactoretinalis, described in *Astronotus ocellatus* by Springer and Mednick (1985), situated at the ventro-caudal juncture of the olfactory bulb and the telencephalon.

It should be mentioned that the retinopetal cells of the nucleus thalamoretinalis, also described by Springer and Mednick (1985), were not found although the fibres within VMdOT in the caudal pretectal area lateral of AO inner-

Fig. 3A. Axial optic tract (AxOT) just caudal of its bifurcation from the marginal optic tract in *L. chrysostomus*. Scale bar = 125 μ m. **B** Preoptic area showing innervation of the contralateral suprachiasmatic nucleus (SN) and the bifurcation of AxOT from the marginal optic tract (MOT). Scale bar = 125 μ m. **C** Marginal optic tract showing its division into the medial optic tract (MdOT). Note the pattern of striations of MOT possibly caused by the pleated optic nerve. Scale bar = 500 μ m

vated a dense nucleus (Figs. 2L; 3C). This may have constituted the retinopetal nucleus but the cobalt may not have labelled the cells due to insufficient transport.

Discussion

This is the first study to examine the retinofugal projections of the red-throated emperor, *Lethrinus chrysostomus* (Perci-

formes). The sensitive cobalt-lysine technique has enabled tracing of both the fine ipsilateral projections which terminate in the suprachiasmatic nucleus and the hypothalamus and the contralateral projections which terminate in the preoptic, thalamic and pretectal nuclei as well as the optic tectum.

The longitudinal bands of light and dark-staining fibres is a striking feature of the marginal optic tract at the level of the optic chiasm. These bands do not appear to be fasciculated but may be a repeating pattern of thick and thin axons in a highly pleated nerve which differentially accumulate cobalt sulphide. This lamination of some parts of the optic tract has previously been observed in the teleost *Channa micropeltes* (Channiformes) (von Bartheld and Meyer 1988) and is postulated to occur at a level where a reorganization of fibres on their route to the optic tectum takes place (Scholes 1979, 1981; Bunt 1982). If this lamination reflects a retinotopic reorganization of optic fibres before they project to the optic tectum (Walsh and Guillery 1984; Collin and Collin 1988), one would expect the lamination to be most prevalent within the optic tracts projecting to the primary termination areas of the tectum. This follows since this lamination pattern persists caudally within the ventral division of the marginal optic tract, which dorsally supplies all of the white and gray zone of the optic tectum, but is not present in the dorsal division of the marginal optic tract (MOTd).

The optic tract of *L. chrysostomus* divides to form a number of optic fascicles. The marginal optic tract divides to form the axial optic tract, the dorsal, intermediate and ventral optic tracts, the medial optic tract, the olfactoretinal tract and the ventromedial optic tract. Whether the axial optic tract (fasciculus ventromedialis tractus opticus of Springer and Mednick 1985 and fasciculus medialis tractus opticus of Fraley and Sharma 1984) is distinct from the ventromedial optic tract (VMdOT of this study) is unknown. Certainly some fibres of the axial optic tract, in this study, rejoin the marginal optic tract at the level of the nucleus of the basal optic root. However, periventricular nuclei and the optic tectum are innervated via a separate pathway which leaves MOT at similar levels but projects caudally. Anders and Hibbard (1974) found a comparable pathway in *Cichlasoma biocellatum*, but considered their fasciculus medialis nervi optici (FMNO) separated from the marginal optic tract a second time to innervate the tectum. In a recent study by von Bartheld and Meyer (1988), the ventromedial optic fascicle (fVMO) was also found to supply the deep tectal layer (stratum album centrale) and may be a comparable tract to the ventromedial optic tract (VMdOT) of this study. In those species thought to possess this tract, its origin has not been determined. Fernald (1982), Braford and Northcutt (1983) and Ekström (1984) thought these fibres originated from the medial optic tract. However, this study reveals that this tract represents an independent fascicle in *L. chrysostomus*, and as in *Channa micropeltes* (von Bartheld and Meyer 1988), appears to originate in the ventral division of the marginal optic tract, although in *L. chrysostomus* it diverges more caudally.

Complex mechanisms must exist to account for the divergence of so many optic tracts caudal of the optic chiasm. As postulated by Presson et al. (1985), sub-populations of axons from the same retinal region may follow different chemicals or respond differentially to a single set of chemical cues. This active guidance mechanism (Meyer and

Fig. 4A. Transverse sections of the pretectum showing a folded nucleus pretectalis superficialis pars parvocellularis (*PSP*) in *L. chrysostomus*. Note that only a few fibres pass through the pars magnocellularis division (*PSM*) of this nucleus. Scale bar = 500 μ m. **B, C** Optic tectum (*TeO*) showing contralateral fibres entering the superficial layer of the superficial white and gray zone (*SWGZ*) (arrowed), four sublaminae of the *SWGZ* with a few fibres projecting into the Deep White Zone (*DWZ*). Scale bars = 125 μ m

Sperry 1976) may also work in association with structural cues (Horder and Martin 1978) or a combination of both (Scholes 1981).

The premise that retino-recipient nuclei receive input from specific sub-populations of retinal ganglion cells may be also influenced by these factors. Little is known about functional parallel processing in teleosts due to the small number of studies relating the topography of retinal ganglion cells to their central termination sites. The topography

of the retinal ganglion cell layer in *L. chrysostomus* reveals a pronounced streak of high cell density (5.0×10^4 cells per mm^2) across the horizontal meridian of the eye with a temporal area centralis of lower density (3.5×10^4 cells per mm^2 , Collin and Pettigrew 1988b). The predominance of a retinal streak is also found in conjunction with a large optic tectum (Fig. 1). This correlation has previously been found in six other Perciformes with pronounced horizontal streaks (Collin 1987), and in *Navodon* (Balistidae), by Ito and Murakami (1984) who found this species to possess an increased band of ganglion cell density across the horizontal axis of the eye. The optic tectum of *Navodon* is correspondingly larger than that of *Sebastiscus* (Scorpaenidae) which has the same sized eye and concentric arrangement of iso-density contours. It is interesting to note that although there is little known of the retinal topography of *Channa micropeltes* (Channiformes), it also possesses a large optic tectum (Bartheld and Meyer 1988). The explanation for this in teleosts is still unknown, especially with relation

to the lamination and supposed retinotopic reorganization of optic fibres within the optic nerve (Collin and Collin 1988) and pretectal regions of the brain. However, in owls, Bravo and Pettigrew (1981) found large and medium-sized ganglion cells in temporal retina, including cells in the area centralis, project to the thalamus while a heterogeneous group of cells, including small and very large neurons, within the horizontal streak project to the optic tectum.

Systematic studies of retinal termination sites has recently shown that different regions of the retina have specific central inputs (Presson et al. 1985; Fraley and Sharma 1984; Springer and Mednick 1985). The suprachiasmatic nucleus contains axons solely from central retina above the optic papilla in *Haplochromis* (Presson et al. 1985) while in *Carassius* this nucleus receives axons from all retinal quadrants with the ventral hemiretina contributing a larger proportion of fibres (Fraley and Sharma 1984). Presson et al. (1985) find no retinotopic organization of fibres in the medial optic tract in *Haplochromis* but, in *Carassius* (Fraley and Sharma 1984), the nucleus opticus dorsolateralis (nucleus of the ventrolateral thalami of this study) and to a lesser degree the nucleus of the posterior commissure (nucleus pretectalis periventricularis pars dorsalis of this study) are organized retinotopically. In addition, the central pretectal nucleus receives axons from the ventral hemiretina in *Haplochromis* (Presson et al. 1985) and the dorsal and ventral retinal quadrants in *Carassius* (Fraley and Sharma 1984). Further study is required to establish whether the optic nerve of *L. chrysostomus* is retinotopically organized and if retinorecipient nuclei receive input from specific subpopulations of retinal ganglion cells, but a strong correlation certainly exists between the size of the optic tectum and an increase in the density of retinal ganglion cells across the horizontal meridian of the eye. A study (Collin and Collin 1988) on the sandlance, *Limnichthys fasciatus* has also found that the elongated optic nerve may be retinotopically organized where the smaller optic axons presumably from the densely-packed retinal ganglion cells of the deep convexiculate fovea lie in close apposition for the length of the optic nerve.

Therefore, since the teleost optic nerve is retinotopically organized (Scholes 1981; Vanegas and Ito 1983) and possesses multiple central targets, the findings in mammals that all major ganglion cell classes project to some central nuclei (Fukuda and Stone 1974; Hickey and Guillery 1974; Wilson and Stone 1975) while only specific subsets of cells project to others (Dreher and Sefton 1979; Leventhal et al. 1981; Rowe and Dreher 1982a, b) may also hold for lower vertebrates.

The lateral geniculate nucleus, renamed the nucleus pretectalis superficialis, pars parvocellularis (PSP) by Braford and Northcutt (1983) since it does not send fibres to the telencephalon (Ito and Kishida 1978; Grover and Sharma 1979; Ebbesson 1980; Northcutt and Braford 1984), is also retinotopically organized in *Carassius* (Fraley and Sharma 1984; Springer and Mednick 1985) and *Haplochromis* (Presson et al. 1985). The complexly folded PSP of *L. chrysostomus* is thought to be primitive or pleiomorphic for teleosts (Northcutt and Wullimann 1988).

Ipsilateral projections have been found in a number of teleosts (Voneida and Sligar 1976; Reperant et al. 1976; Peyrichoux et al. 1977; Ebbesson and Ito 1980; Springer and Gaffney 1981; Prasada Rao and Sharma 1982; Springer and Mednick 1985; Fritzsche et al. 1987) and are present

in at least some adults of all vertebrate classes (Ebbesson 1984). It is clear that in most modern teleosts ipsilateral projections have been either lost or reduced from the large bilateral projections of the ancestral ray-finned fishes (Braford and Northcutt 1983) and *L. chrysostomus* is no exception. Only two small groups of fibres recussate across the horizontal commissure to innervate the ipsilateral suprachiasmatic nucleus and the nucleus lateralis hypothalamus. However, it has recently been found that in a number of advanced teleosts, viz. the sockeye salmon, *Oncorhynchus nerka* (Ebbesson et al. 1988), the cichlid, *Haplochromis burtoni* (Fritzsche et al. 1987) and the yellow-finned bream, *Acanthopagrus australis* (unpublished results), striking differences exist between the ipsilateral retinofugal projections in adults and juveniles of the same species.

The subdivision of optic fascicles terminating within a thin superficial layer, a thick superficial white and gray zone (SWGZ), a sparsely innervated central zone and the deep white zone of the optic tectum, has previously been found anatomically (Northcutt 1983) and physiologically (Schmidt 1979) in *Carassius*. The SWGZ is also subdivided into four darkly staining layers. Although the entire layer is labelled, the larger diameter fibres reveal a laminar appearance with the thickest fibres lying nearer the superficial layers. This subdivision (see review by von Bartheld and Meyer 1987) is well developed in advanced teleosts but its functional significance is unknown. Northcutt (1983) suggests that each fibre layer consists of different receptive field classes of optic fibres or each layer may contain additional classes of bipolar neurons from the central zone.

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